August 2017

A Hemimysis Driven Novel Ecosystem at a Modified Boulder Breakwall

Eric John Geisthardt
University of Wisconsin-Milwaukee

A HEMIMYSIS DRIVEN NOVEL ECOSYSTEM AT A MODIFIED BOULDER BREAKWALL

by

Eric J. Geisthardt

A Thesis Submitted in

Partial Fulfillment of the

Requirements for the Degree of

Master of Science

in Freshwater Science and Technology

at

The University of Wisconsin- Milwaukee

August 2017

ABSTRACT

A HEMIMYSIS DRIVEN NOVEL ECOSYSTEM AT A MODIFIED BOULDER BREAKWALL

by

Eric Geisthardt

The University of Wisconsin-Milwaukee, 2017
Under the Supervision of Professor John Janssen

The US Army Corps of Engineers (USACE) is mandated to maintain and repair aging breakwall structures in all commercial ports on the Great Lakes. In May of 2014, the construction of Milwaukee Harbor USACE “green” breakwall (GBW) reconciliation created complex rocky aquatic habitat by depositing cobble-sized stone as a veneer over standard 6-10 ton boulders, thus creating “control” (boulder) and “treatment” (cobble) habitats. The breakwall is home to a prolific population of *Hemimysis anomala*, the introduced Ponto-Caspian mysid, which is significantly more abundant on cobble versus boulders ($p<0.05$, using a novel trap for *Hemimysis*). Fish and forage communities were sampled in 2015 and 2016 using a combination of experimental and micromesh gill nets, night scuba diving surveys, and a novel *Hemimysis* trap. This nearshore lithophilic mysid appears to provide a significant new seasonal food resource in the Milwaukee Harbor for pelagic prey fishes during inshore spawning migrations and upwelling events. Alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) fed heavily on *Hemimysis* with some individuals consuming hundreds of mysids. Night scuba diving surveys and gill netting confirmed that rainbow smelt preferred to forage on the cobble section ($p<0.05$), and also consumed more *Hemimysis* there than they did at the control breakwall site ($p<0.05$). *Hemimysis* were also the primary food item consumed by nearshore game fishes such as YOY yellow perch (*Perca flavescens*), YOY largemouth bass (*Micropterus salmoides*), and juvenile rock bass (*Ambloplites rupestris*) caught at the breakwall. This study provides the first documented evidence that where abundant in the Laurentian Great Lakes, *Hemimysis* do have the ability to significantly impact local food webs and drive the feeding ecology of both pelagic transient and nearshore resident fishes.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

I would like to sincerely thank all of incredible friends, family, and faculty who have been a part of my life during my time here at UWM. It is with a great deal of gratitude that I say I would never have made it without your support and encouragement. This project would not have been possible without Burton Suedel and the support of the US Army Corps of Engineers in facilitating this research I was fortunate to be a part of. Also thanks to Salmon Unlimited for their scholarship contribution. Standard thanks to Ryan Glasford, Chris Groff, and D'Chester for just giv'n er while contributing to my field work and data collection in 2016. Fellow and former graduate students Brennan Dow, Chris Suchocki, Dylan Olson, and Ben Turschak are also deserving of thanks for their assistance in the field and guidance during my tenure here at UWM. None of this would have been possible without John Janssen. Thank you for taking me on as a student, helping me grow as a scientist, and opening my eyes to a world of possibilities. Most of all I'd like to express my deepest gratitude to my parents, Jim and Judy Geisthardt, for taking my brother and I to swim at the beaches where I first fell in love with Lake Michigan. The same intrigue that captivated me as a child standing on the shore looking out is that which still drives me to dive below the surface and keep exploring the life aquatic and all its endless possibilities. Finally, I'd like to dedicate this thesis to my cat Finn for his continued love and support in tough times.

After that, shrimpin was easy

Introduction

Artificial reefs have been popular tools designed to enhance aquatic environments and fishing activities since the early 1900s (Stone 1974). Early reefs constructed in coastal marine environments were primarily intended to benefitting recreational fishing, and were often quite popular with anglers (Stone 1974; Buckley 1982). As reef constructing increased, fisheries managers and researchers began to focus on their impacts on aquatic ecosystems and the biological community in addition to the perceived benefits for recreational fishing (Stone 1982). At the same time, research on artificial reefs in freshwater was expanding with studies often indicating significantly higher catch rates on artificial reefs than control areas (Crumpton and Wilbur 1974). By 1977, Prince et al. indicated that over 60% of state agencies were using artificial reefs in their management of freshwater fisheries. Thus, there has been interest in constructing artificial reefs in the Great Lakes for some time (D'Itri 1985).

Natural rocky habitats in Lake Michigan are diverse and include glacially polished bedrock, glacial grooves in such bedrock typically infilled with cobble, talus slopes, and glacial deposits such as drumlins which all vary in the size and abundance of interstices (Waples et al. 2005; Janssen et al. 2005; Riley et al. 2014, 2017). Rocky substrates are important to benthic and epibenthic organisms for both adherence and cover. In Lake Michigan, rocky habitats are historically known as important spawning habitat for lake trout (*Salvelinus namaycush*) (Marsden et al. 1995) and yellow perch (*Perca flavescens*) (Robillard and Marsden 2001), and have recently been linked to important seasonal feeding ecology of important forage and sport fishes (Janssen and Luebke 2004; Janssen et al. 2005; Kornis and Janssen 2011). Adequate interstitial space in Great Lakes reefs is important for a variety of aquatic species, and is essential for spawning lake trout and as cover for crayfishes, mottled sculpin, and round gobies (*Neogobius melanostomus*) (Janssen and Quinn 1985; Marsden et al. 1995; Ray and Corkum 2001).

Several of the most impactful Ponto-Caspian invasives such as zebra mussels (*Dreissena polymorpha*), quagga mussels (*Dreissena bugensis*), round gobies, and the amphipod *Echinogammarus ischnus* which have colonized the Laurentian Great Lakes in recent decades are lithophilic and have significantly altered rocky habitats and the trophic structure of Lake Michigan (Ricciardi and MacIsaac 2000; Vanderploeg et al. 2002; Cuhel and Aguilar 2013; Turschak et al. 2014; Rogers et al. 2014). The increased importance of benthic productivity of rocky nearshore areas has led to recent focus on their impacts on food web ecology and novel energy subsidies for important forage fish such as alewife (*Alosa pseudoharengus*) (Janssen and Luebke 2004; Kornis and Janssen 2011). The recently introduced bloody red shrimp, *Hemimysis anomala* (henceforth *Hemimysis*), a lithophilic epibenthic mysid with a strong affinity for interstices has successfully colonized natural and artificial reefs in Lake Michigan. *Hemimysis* are known to cause significant changes in food web dynamics and trophic structure where they have been introduced elsewhere outside their native range (Ketelaars et al. 1999; Borcherding et al. 2006), but such effects are poorly documented in the Great Lakes despite a widespread distribution.

The US Army Corps of Engineers (USACE) is mandated to maintain breakwalls important for navigation in commercial ports throughout the Great Lakes. Typical repairs consist of adding large boulders to existing structures as reinforcement to withstand powerful waves. As part of a pilot program for creating reef habitat during routine repairs, an artificial reef was designed as an ecologically enhanced “green” breakwall (henceforth GBW), and constructed by the USACE along the inside of Milwaukee Harbor’s outer breakwall through a modified design with cobble substrate as a veneer over a typical boulder repair. Past Great Lakes artificial reef projects have primarily focused on creating new rocky habitat (Rutecki et al. 1985; Kelch et al. 1999; Creque et al. 2006; Houghton 2014) rather than enhancing the ecological value of the numerous existing manmade structures through reconciliation projects as has often been a goal in marine breakwall settings (Mooschella et al. 2005; Scyphers et al. 2014).

Evaluation of the GBW was a two-step process, an initial plan was executed and modified during 2015, and substantial modifications were made for 2016. The initial focus was on the GBW's value as a potential spawning site for lake trout and yellow perch, while determining whether collective knowledge of natural reef ecology and prior artificial reef construction in the Great Lakes could inform me as to the food web ecology and benthic community that would emerge at the Milwaukee Breakwall. However, the unanticipated importance of *Hemimysis* in the food web was significant enough to shift many of my sampling methods to focus on understanding their role at the breakwall.

My objectives were to evaluate the developing GBW food web versus an adjacent reference (REF) site, and to determine whether locally abundant *Hemimysis* were impacting the food web dynamics and feeding ecology of fishes occupying the Milwaukee Breakwall.

METHODS

Physical assessment

Study Area

The GBW is a section of modified boulder breakwall (quarried limestone) located along the inside of Milwaukee Harbor's outer breakwall, between 150 and 300 meters south of the North Gap. (Fig. 1). The 150m long GBW was constructed using 10-40 cm subangular cobble as a veneer over the top of 6-10 ton boulders required as structural support for breakwall repairs. Limestone boulders were deployed in 2013 and the cobble veneer introduced in April-May of 2014. The top of the GBW cobble lies at <2 meters in depth depending on lake levels and tapers to a depth of about 7 meters where the cobble quickly transitions to silty sediments comprising much of the harbor's benthos. Original designs (Fig. 2) called for the placement of a spawning inlay comprised of smaller rocks (10-20cm) along the top of the GBW. However, a majority of the spawning inlay and cobble veneer is at a critical angle of repose resulting in rockslides and periodic shifting due to powerful waves cresting the breakwall during fall storms. Engineers also incorporated ridges and swales during construction resulting in the heterogeneous habitat at the southern end of the GBW.

The Reference Site (REF) was an adjacent 150m section of boulder breakwall inside the harbor (Fig. 1) which was repaired using placement of 6-10 ton boulders at the same time the 6-10 ton boulder base and cobble veneer of the GBW was installed. This location was selected as a reference due to the likelihood of experiencing similar hydrologic and thermal conditions throughout the season, as the currents and temperature regime were anticipated to have a significant influence on the fish species utilizing of the breakwall. The section of boulders south of GBW was partially deposited after the GBW and REF boulders, so was not suitable for comparisons.

Physical assessment of initial construction was conducted in 2014 via multibeam sonar bathymetry by the USACE. In August of 2016 a second assessment of the GBW was conducted by Brennan Dow (UWM) using a Lowrance HDS10-Gen 2 with StructureMap^{TM} HD Sonar Imaging during aquatic habitat mapping efforts in the Milwaukee Harbor. Observations and measurements of physical dimensions of the GBW and REF were also made by SCUBA divers in 2016. A total of 38 dive surveys and 66 snorkel surveys were conducted at the breakwall during 2015 and 2016.

Temperature

Temperature loggers (HOBO Pendant Temperature 64K Data Logger) were deployed at the GBW/REF interface and at the South end of the GBW in May of 2015. Loggers were exchanged via scuba diver or snorkeler in October 2015 and again in June of 2016 to download data and redeploy. Each string of temperature loggers consisted of a shallow logger at 2m, a middle logger at 4m, and a bottom logger at the base of the GBW in 7m of water (Fig. 3). Loggers were individually attached to a lead core line fastened to the breakwall and buried under the cobble to prevent snagging by anglers. Burying the loggers also prevented the shallow loggers from being influenced by direct sunlight which would have skewed daytime temperatures. Loggers recorded at five minute intervals during summer months and at one hour intervals overwinter.

Biological Assessment

Fish Sampling

To compare fish utilization between the GBW and REF, bi-weekly gillnetting took place from June through October in both years. During 2015 experimental mesh gill nets with a range of graded mesh sizes (63.5 mm, 50.8 mm, 38.1 mm, 25.4 mm, 12.7mm. 1.3 height 150m total length) were utilized aiming to catch a wide range of fishes at GBW and REF. However, experimental gill nets were quite lethal to rock bass (*Ambloplites rupestris*) the most abundant resident fish. Although rock bass from gill nets were taken for diet analysis, because they typically have a limited home range (Gerking 1953) it was suspected that repeated experimental gill netting would significantly impact their abundance. In 2016, graded micromesh gill nets (8mm and 6mm stretch; 1.3m height, 61m total length) were utilized to target juvenile alewife from the class of 2015, and other juvenile fishes as it became apparent that the GBW was likely serving as nursery habitat. During the final five nettings of 2016 an additional 15m long gill net panel of 12.7mm stretch x 1.3m height was fished with the graded micromesh nets. This larger mesh served to capture alewife, rainbow smelt (*Osmerus mordax*), and yellow perch which had outgrown the 8mm stretch mesh as the summer of 2016 progressed.

Sampling locations were the same for all nets set at the GBW and REF over the course of both field seasons. Nets were set along the rocky slope in approximately 2-3m of water at both sites to limit thermal variation's influence on catches. All gill nets were fished overnight from approximately 1600 to 0800 and pulled in the same order as they were deployed to ensure equal sampling times. Nets were pulled by hand and immediately covered with ice in separate bins. Captured fish were promptly picked from the net at shore and live fish were euthanized with an overdose of MS-222. Fish were then immediately preserved in 95% ethanol to halt digestion and preserve stomach contents. All fish collected were sorted by species, enumerated, and the standard and total length to the nearest millimeter was recorded from a subsample of up to 10 fish per species per site which were separated for later stomach content analysis.

Gee-minnow traps were used in 2015 to sample round goby abundance at both sites. Five baited minnow traps were set at each the GBW and REF to augment gill netting efforts. Traps were set and retrieved by snorkelers. Round gobies and bycatch were counted and both total and standard length were recorded.

Night Dives

Night dives were conducted twice in 2015 and seven times in 2016. The first night dive was exploratory and investigated the behavior of *Hemimysis*, which I was finding to be an important constituent in rock bass and alewife diets, yet went unobserved during daytime dives until August of 2015 at which time they commonly formed swarms in boulder caves. In 2016, protocols were established to standardized fish observations along paired transects. During night dives a pair of divers armed with a dive slate, video recorder, and dive lights would work together with one surveying a shallow transect (<4m), and the other surveying a deep transect (>4m to base of rocks). Transects consisted of five, 30m sections marked with submerged buoy lines on both the GBW and REF for comparison. At the end of each 30m segment divers surfaced, recorded the number of all fish species and crayfish observed along with any other notes. The direction that transects were run (North or South) as well as deep vs. shallow diver was determined randomly. Video was recorded for further documentation and illustration. Alewife numbers were not recorded during night dives as their high mobility and schooling nature made counting and distinguishing between the same fish multiple times impossible.

Diet Study

Analysis of stomach contents was used to examine the developing food web of the breakwall and address whether foraging behavior or diet was different among fish caught at the GBW and the REF. Following each gill net set a subsample of 10 fish per species per site were separated for stomach content analysis and preserved in 95% ethanol. If fewer than ten fish of a species were caught, then all stomachs were removed for analysis. Contents were analyzed under a dissecting microscope, enumerated, and each item was identified to the lowest practical taxa. In the case of round gobies which lack a defined stomach the entire digestive tract was examined.

Hemimysis Study

I developed a novel funnel trap for sampling *Hemimysis* in rocky habitats which also functions effectively at a variety of substrates, depths, and population densities. Vertically towing plankton nets adjacent to dock walls after laying several minutes on the bottom has been used as an effective way to capture this mobile lithophilic mysid (Walsh et. al. 2010, Taraborelli et. al. 2012, and Yuille et. al. 2012). However, the GBW and REF are slopes, that would not allow vertical plankton tows. After preliminary tests in late 2015, in 2016, traps were constructed consisting of black 7.6 liter buckets with a large funnel affixed inside their lids into which a 15cm diameter hole had been cut. The tip of the funnel was trimmed back to leave a 2cm diameter funnel opening into the bucket to alleviate fouling. A window sash weight was affixed to the bottom of the bucket to ensure traps would remain in place. Traps were deployed by divers or snorkelers who ensured the weight and trap were firmly fixed in the substrate. At the REF, traps were deployed by dropping the sash weight into a crevice between boulders to wedge the trap firmly in the cavity. Deployments were made on the same day as gill net sets with five traps on the GBW and five at the REF. Captured *Hemimysis* were sorted into juveniles, adult males, and adult females to assess population structure. Several *Hemimysis* stomachs and fecal pellets were examined from September of 2015 and 2016. Their contents were examined to generate a diet list but not enumerated as few hard structures remained intact.

Rock Collections

Whole rock collections were made on 24 September, 2015, 1 July, 2016, and 4 October, 2016 to assess the maturation of the benthic invertebrate community on the newly placed cobble of the GBW. Due to the lack of collectable sized rocks present at the REF no samples were taken there. Similar sized rocks (8-20cm diameter) were collected by scuba divers on all three occasions by quickly sealing the rock in a cloth bag fastened shut with a cable tie. A total of 12 rocks were collected during each sampling event however one rock was misplaced during October of 2016 and only 11 were processed. These samples were processed by rinsing each rock and its bag over a 500µm sieve to capture benthic macroinvertebrates attached to the rocks and mussel matrix. Each rock was also scraped clean of any mussels and accompanying macroinvertebrates which were then preserved in 95% ethanol for identification and enumeration. Samples were sorted and processed under a dissecting microscope then identified to the lowest practical taxa.

Statistical Analyses

All ANOVA analyses were run using Systat 10.2 and paired t-tests were conducted using Excel.

Fish Sampling

Two-factor analysis of variance (ANOVA) was used to compare log(n+1) transformed round goby catches from minnow traps at both sites with Site and Date as the independent variables. This also tested for the effect of Site*Date interactions as well as each of these main effects.

Two-factor ANOVAs were also used to compare log(n+1) transformed gillnet catches from 2016 of round goby, rainbow smelt, alewife, and yellow perch as these species were the only ones caught on enough dates for comparison. For these tests, Site becomes the fixed independent variable and date becomes the random replicator due to variations in environmental conditions.

A Paired T-test was also run to compare the total lengths of rock bass caught at the GBW and REF.

Night Dives

The number of rock bass and rainbow smelt observed during night dives at each site was used to conduct a three-factor ANOVA with Site, Date, and Depth as independent variables. This tested for the effect of Site*Date, Site*Depth, Date*Depth, and Date*Depth*Site interactions as well as each of these three main effects.

I also tested whether rock bass and rainbow smelt were consistantly encountered at any certain transects on the GBW and REF. An ANOVA with Date, Depth and Depth*Date and Section as variables was run to determine whether either species presence was biased towards specific sections of the transect surveyed

A two-factor ANOVA was run on the mean number of rock bass at shallow transects at both sites to analyze effects of Temperature, Site, and Temperature*Site interactions.

Diet Study

To analyze the consumption of *Hemimysis* by alewife, rock bass, and rainbow smelt in 2016 at each site two-factor ANOVAs were conducted with Date and Site as independent variables and the log(n+1) transformed number of *Hemimysis* consumed as the dependent variable to determine differences in foraging between the sites. This tested for the effect of Site*Date interactions as well as each of these main effects. Individuals with empty stomachs and dates without paired fish samples were excluded from analysis.

To assess the overall diet composition and foraging preferences in commonly encountered fish, frequency of occurrence ($\%F_i$) and numeric proportion (P_i) were calculated.

$$\%F_i = (N_i/N) \times 100 \qquad \text{and} \qquad P_i = S_i/S$$

Where N_i = the number of a species with food item *i* in their stomach and N = the total number of fish with stomach contents, and S_i = the total combined number of food item *i* in the stomachs of a species and S = the total combined number of all food items consumed by that species.

Juvenile alewife <90mm TL were separated from larger adults for the purposes of stomach analysis as these smaller fish were all likely age <1. The 90mm cut off for juveniles was established because the length histogram of dissected alewives indicates a tightly grouped year class up this length (Fig. 4), and 90mm was also the maximum size reached by a known age alewife of the 2015 year class before YOY from 2016 first showed up in gill nets. Because not all alewives were aged, no statistical analyses were run to compare age <1 alewife to adult alewife.

Hemimysis Study

Two-factor ANOVAs were run on the contents of *Hemimysis* traps set during 2016 with Date and Site as independent variables and log(n+1) transformed *Hemimysis* catch divided into five subcategories of Total *Hemimysis*, Juvenile *Hemimysis*, Adult *Hemimysis*, Male *Hemimysis*, and Female *Hemimysis* each analyzed as dependent variables. This tested for the effect of Date, Site, and Site*Date interactions for each of these dependent variables.

Three-factor ANOVAs with Date, Site, and Trap Number as independent variables and log(n+1) transformed *Hemimysis* catch divided into five subcategories of Total *Hemimysis*, Juvenile *Hemimysis*, Adult *Hemimysis*, Male *Hemimysis*, and Female *Hemimysis* each analyzed as dependent variables were also run to test whether specific trap location effected the catches of each subcategory of *Hemimysis*.

Rock Collections

To analyze the numbers of chironomids and amphipods (*Echinogammarus ischnus*) collected on whole rock samples at the GBW from 4 October, 2015, 1 July, 2016, and 24 September, 2016 a one-factor ANOVA was conducted with date as the fixed independent variable and log(n+1) transformed invertebrate counts as the dependent variable. Post-hoc Tukey HSD Multiple Comparison tests were used for pairwise comparisons between dates.

RESULTS

Physical Assessment

The physical structure and stability of the GBW was an initial concern for diving and snorkeling survey work due to potential rockslides and settling. During 2016 diving surveys it was confirmed that both cobble and large boulders had been subject to significant changes in position due to movement of ice flows and wave action during intense winter storms. A transect line left at the top of the GBW over winter in 2015-2016 was found buried by cobble which had slid down the slope as much as three meters. Several large boulders had also been dislodged from above the water line were found near the base of the GBW. Analysis of 2016 side scan imagery confirmed these observations. Continued settling of rocks at the GBW may have significant impacts on the benthic community as it develops. Currently the cavities in the cobble present at the GBW range from 2-20cm across and measure up to three meters in depth. Cavities at the REF between large boulders were much larger at 0.5-2 meters across and of similar depth.

Temperature

Temperature fluctuations at the GBW were of interest because of the study area's proximity to the North Gap makes it quite vulnerable to seiche and upwelling events causing rapid change in water temperature. Mixing of lake and harbor water masses has the potential to cause significant temperature fluctuations and changes in fish behavior, feeding, and depth distribution (Magnuson et al. 1979; Brandt et al. 1980). Paired strings of temperature loggers deployed from June 2015 to October 2016 indicate that the thermal regime at the GBW and REF varied by less than 2°C at all times throughout the course of the study. Cold water upwelling events were frequent in both 2015 and 2016 and sometimes prolonged for several weeks (Fig. 3). The intensity of upwelling varied but at times caused temperature fluctuations of up to 12°C over 24 hour periods in both years. A thermocline was often present at the beginning of an upwelling event as cool lake water intrusions made their way into the harbor. During strong upwellings a vertical thermocline was often present at the North Gap with cold lake water at the surface outside the harbor and warm river water inside of the breakwall. An unusually intense upwelling during late August of 2015 pushed warm surface waters over 40km offshore and dropped surface temperatures throughout Milwaukee Harbor from 22°C to 8°C for several consecutive days (Fig. 3) causing most fish to vacate or become inactive.

Fish Sampling

Gillnetting efforts in 2015 and 2016 revealed a diverse assemblage dominated by the six most common species at both sites making up >98% of the total catch (Table 1). A total of 19 species were caught at the GBW and 13 at the REF (Table 1). Eight of which were known only from a single collection. Alewife and round goby were respectively the most abundant fish in both 2015 and 2016 although different mesh sizes of gill net were used each year. Alewife were more abundant in micromesh nets used in 2016 due to the large class of yearling alewife which were highly susceptible to the mesh sizes used (Table 1).

At the GBW alewife comprised 51.3% of gill net catch in 2015 and 51.8% of gill net catch in 2016. At the REF alewife comprised 61.2% of gill net catch in 2015 and 64.3% of gill net catch in 2016.

Round goby catches in minnow traps in 2015 were highly variable at both sites (Fig. 5). The two-factor ANOVA had a not significant Site*Date interaction ($F_{16,132}$=0.69, p=0.8). Both of the main effects were significant (Site: $F_{1,132}$=4.55, p=0.035) (Date: $F_{16,132}$=2.18, p=0.008). Gill net catches from 2016 were also variable with slightly more round gobies present at the GBW (Table 1). At the GBW round goby comprised 36.5% of gill net catch in 2015 and 24.2% of gill net catch in 2016. At the REF round goby comprised 27.4% of gill net catch in 2015 and 21.7% of gill net catch in 2016. However, the two-factor ANOVA run on gill-net catches had not significant effects for either Site: ($F_{1,13}$=1.15, p=0.303), nor Date: ($F_{13,13}$=2.06, p=0.102).

Alewife were the only species caught during every gill net set, as well as the most abundant species at each site in both years (Table 1). The two-factor ANOVA had no significant effects for either Site: ($F_{1,13}$=0.039, p=0.846), nor Date: ($F_{13,13}$=1.26, p=0.343). Almost all alewife age <1 were caught during 2016 due to the large year class produced in 2015 and the increased sampling effort with micromesh gill nets that year.

Rainbow smelt were the third most abundant species caught in micromesh nets at both sites in 2016 (Table 1). Rainbow smelt may have been present often during gill netting in 2015 but were not susceptible to the larger mesh of experimental gill nets used in 2015 (Table 1). The two-factor ANOVA showed a significant effect for Date: ($F_{13,13}$=9.087, p<0.001) and Site: ($F_{1,13}$=13.65, p=0.003) with over twice as many rainbow smelt being netted at the GBW than at the REF in 2016. Catch in gill nets was quite variable but was highest during prolonged upwelling events when cool water was present at the GBW for several consecutive days (Fig. 6A and 6B).

Rock bass were sampled almost exclusively in experimental gillnets in 2015, while micromesh nets set in 2016 avoided lethally sampling this most abundant resident fish (Table 1). Rock bass caught at the GBW were generally smaller than those at the REF (mean TL 159mm and 167mm respectively, Table 2 and 3) although a paired t-test indicated they were not significantly different (df=60, t=1.3 p=0.099). During night dive the smallest rock bass were always encountered at the GBW, with very few small rock bass present at the REF. Although quantitative length data was impossible to obtain during such sampling, the frequency of small rock bass noted by divers was much greater at the GBW.

Yellow perch catch was almost entirely from micromesh nets set in early September 2016 when YOY yellow perch typically become demersal after drifting pelagically as fry (Beletsky et. al. 2007). The two-factor ANOVA showed a significant effect for Date: ($F_{13,13}$=13.22, p<0.001), but no significant effect for Site: ($F_{1,13}$=0.708, p=0.415).

Night Dives

During night dives, the two species most easily counted were rock bass and rainbow smelt which were often seen hovering over substrate and not actively swimming. Alewife were commonly seen but highly active, and divers were not able to accurately count and distinguish between individual fish due to this mobility. Round gobies were frequently observed at the breakwall hiding in complex crevasses not easily surveyed, and often returned to cover out of sight of divers when startled. Due to this behavior and the inability to accurately count round gobies their numbers not recorded.

Night dives revealed important behavioral aspects of the fish and *Hemimysis* utilizing the GBW and REF that were not otherwise observed during gill netting or day time dives and snorkels. For example, during the initial night dive on 8 July, 2015 I first observed the emergence of *Hemimysis* from the cavities in the cobble of the GBW shortly after dusk. Until this point no *Hemimysis* had been observed other them those contained in rock bass stomachs. Divers repeatedly observed this extracavernal migration of

Hemimysis during every night dive conducted even when densities were low and swarming behavior was not present. Often divers observed few *Hemimysis* at the start of dives between 20:00 and 21:00, while more were seen towards the end of dives between 22:00 and 24:00. The most important fish observations made during night dives were those related to the behaviors of rock bass and rainbow smelt. For example, at night divers observed rock bass occupying cavities at the surface of the reef while they may have been hidden from view deep in the reef during the day. Additionally, rainbow smelt observed by divers at the GBW and REF were exclusively present at night.

Rock bass were most commonly observed along the shallow transects at both sites, and sightings increased in relation to water temperature (Fig. 7). The significant interaction between Site*Temperature ($F_{1, 10}$= 5.28, p=0.044) from a two-factor ANOVA indicates that the positive relationship between increased temperature and mean rock bass/transect was greater at the GBW than at the REF. Further evaluation of rock bass utilization of the GBW and REF was done after a cursory look at the data appeared to indicate that more rock bass might have been consistantly encountered at certain transects. To determine whether rock bass were indeed more common at any individual transects I ran an ANOVA with Date, Depth, Depth*Date, and Section as variables. At the GBW, Section was not significant ($F_{4, 52}$= 1.93, P=0.12) but Date ($F_{6, 52}$= 8.13, P=0.00), Depth ($F_{1, 52}$= 51.49, P=0.00), and Depth*Date($F_{6, 52}$= 3.92, P=0.00) were significant. At the REF, Section ($F_{4, 52}$= 1.76, P=0.15) and Depth ($F_{1, 52}$= 3.95, P=0.052) were not significant, while Date ($F_{6, 52}$= 5.39, P=0.00), and Depth*Date($F_{6, 52}$= 4.55, P=0.00) were significant.

After determining there were not significant differences between transect sections and rock bass observations I ran a three factor ANOVA. The full analysis is in Table 4. Results confirm that there was a significant Site*Depth interaction ($F_{1,112}$ = 8.19, P = 0.005). Rock bass position at both the GBW and REF was often related to the presence and depth of the thermocline. Complexity was indicate by the significant Site*Depth*Date interaction ($F_{6,112}$ = 3.33, P < 0.005) indicating complex interactions affected rock bass utilization of the breakwall.

I also tested whether rainbow smelt consistantly encountered at certain transects in the same manner as was done for rock bass. I ran an ANOVA with Date, Depth and Depth*Date and Section as variables. At the GBW, Section was not significant ($F_{4, 52}$= 0.678, P=0.61) but Date ($F_{6, 52}$= 2.64, P=0.03), Depth ($F_{1, 52}$= 54.9, P=0.00), and Depth*Date($F_{6, 52}$= 2.6, P=0.03) were significant. At the REF, Section was not significant ($F_{4, 52}$= 2.05, P=0.10) but Date ($F_{6, 52}$= 10.25, P=0.00), Depth ($F_{1, 52}$= 31.6, P=0.00), and Depth*Date($F_{6, 52}$= 10.76, P=0.00) were significant.

I than assumed there was no transect effect and a three-factor ANOVA conducted on log(n+1) transformed night dive observations of rainbow smelt indicated that all interactions between factors as well as the three main effects were significant (Table 4) and the significant Site*Depth*Date interaction indicates complexity. As with rock bass, the complexity seems to be best explained by temperature, particularly the presence and depth of the thermocline. Rainbow smelt were always more abundant along the deep transect in the hypolimnion at both sites and were often <50cm from the bottom.

Rainbow smelt were always more commonly observed at the GBW than the REF with the exception of two dives in early September 2016 (Fig. 6C). During sampling on 6 September, 2016, a small upwelling event was occurring during the duration of the dive were bottom temperatures dropped from 20.3°C before the dive to 17.1°C during the dive (Fig. 6A). The diver along the deep transect first encountered the cool layer of hypolimnetic water intruding into the harbor at the North end of the GBW next to the interface with the REF. All 65 rainbow smelt observed on the GBW were on the Northernmost transect at the leading edge of the hypolimnetic water adjacent to the REF. Continuing onto the REF all 329 rainbow smelt observed on 6 September, 2016 were recorded from the Southernmost transect in part of the same school as those observed on the GBW. As the upwelling hypolimnion intruded into the harbor the largest collective number of smelt from any dive or gillnetting was observed riding the current into the harbor through the North Gap and gaining access to abundant *Hemimysis* present inside the breakwall.

On the 1 September, 2016 night dive the inverse occurred as downwelling increased temperatures from 13°C to 15.3°C (Fig. 6A) during the dive and forced hypolimnetic water out of the harbor causing a thin layer of cold water to be present at the REF and the North end of the GBW.

Other species infrequently observed during night dives include walleye (*Sander vitreus*), white sucker, and juvenile rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). Walleye were almost always encountered at the deep transect laying on the bottom likely waiting to ambush passing forage following the base of the reef. White suckers were commonly seen occupying medium sized cavities in the warmer epilimnion. Juvenile trout behaved most similarly to rainbow smelt, and were often observed hovering above the bottom and slowly navigating the edges of large cavities and cobble containing swarming *Hemimysis* on which they were likely feeding, as several juvenile trout caught in gill nets were found to feed heavily on *Hemimysis.*

Diet Study

Alewife

Alewife fed heavily on *Hemimysis* at both the GBW and REF throughout the sampling period and was numerically the most abundant food item consumed at both sites. Both the frequency of occurrence and proportion of *Hemimysis* in adult alewife guts was greater on the GBW than at the REF (Table 2 and 3). The two-factor ANOVA analyzing *Hemimysis* consumption by alewives showed a significant Date effect ($F_{9,107}$=3.62, p=0.001), but there was no significant effect for either Site ($F_{1,107}$=0.072, p=0.789), nor the Site*Date interaction ($F_{9,107}$=1.747, p=0.087). Chironomids were expected to be quite important to adult alewife but made up only a small proportion of the diet at both sites (GBW: P_i=0.06, REF: P_i=0.05).

Differences in stomach content composition of juvenile and adult alewife were numerically assessed. Juvenile alewife foraged more often on zooplankters and chironomids than larger adults did (Table 2 and 3).

Rainbow Smelt

Rainbow smelt in 2015 and 2016 fed primarily on *Hemimysis* at both sites (P_i =0.77 at GBW and P_i=0.46 at REF). Rainbow smelt at the REF tended to consume more zooplankton at the REF than they did at the GBW (REF: P_i =0.52, GBW: P_i =0.22). Both the frequency of occurrence and proportion of *Hemimysis* in rainbow smelt guts was greater on the GBW than at the REF (Table 2 and 3). The two factor ANOVA analyzing rainbow smelt consumption of *Hemimysis* indicated significant effects of both Date: ($F_{1,78}$=3.57, p=0.004) and Site ($F_{1,78}$=7.38, p=0.008), but no significant Site*Date interaction ($F_{6,78}$ =0.934, p=0.47).

Rock Bass

Rock bass captured in 2015 gill netting consumed primarily *Hemimysis* at both sites (REF: P_i =0.87, GBW: P_i =0.97). The two factor ANOVA had no significant effects for either Date ($F_{9,14}$=1.52, p=0.233) or Site ($F_{1,14}$=0.282, p=0.604). Because sample size was small and many dates lacked paired data, I could not test for the significance of Site*Date interactions. The second major prey item of rock bass at both study sites were juvenile round gobies which had the same frequency of occurrence as *Hemimysis* (F_i = 43%) in REF fish. At the GBW round gobies were the second most commonly consumed item (F_i = 37%) followed by chironomids pupae (F_i = 19%), and rusty crayfish (F_i = 15%). Larger prey items such as gobies and crayfish were often co-consumed with *Hemimysis*, and although larger fish tended to consume round gobies no clear shift to piscivory was observed.

Yellow Perch

A majority of the yellow perch gillnetted were YOY perch which had recently returned to shore, post-larval drift. As pelagic larvae in Lake Michigan YOY yellow perch feed primarily on zooplankton, making the shift to benthic invertebrates after they return to nearshore habitats. Many of these YOY yellow perch may have been too small to forage on the elusive adult *Hemimysis* but were able to consume juvenile *Hemimysis* which are typically 1-2mm in length, similar size to the mobile Calanoid copepods which yellow perch fed heavily on at both sites (REF: P_i =0.54, GBW: P_i =0.66). A few YOY yellow perch gorged themselves on juvenile *Hemimysis*, with one individual caught on the GBW consuming 291 juvenile *Hemimysis* accounting for 52% of all juvenile *Hemimysis* consumed by yellow perch at the GBW. The same was true at the REF, where four of the yellow perch sampled contained 53% of all juvenile *Hemimysis*.

Largemouth Bass

Few largemouth bass (*Micropterus salmoides*) were sampled at both sites during the study (REF: N=5, GBW: N=13). Those which were netted fed almost exclusively on *Hemimysis* (P_i =0.98 for both sites).

Round Goby

Round gobies were numerous and most frequently fed on dreissenid mussels, their preferred forage (F_i=79% at REF and F_i=70% at GBW). Chydorids were the second most frequently encountered forage, and were numerically the most abundant item in round goby stomachs owed to their small size relative to *Dreissenid* mussels (P_i=71% at REF and P_i=60% at GBW). There were not any significant differences in diet between round gobies occupying the GBW and REF.

Hemimysis Study

Two-way ANOVAs run on Total *Hemimysis*, Juvenile *Hemimysis*, Adult *Hemimysis*, Male *Hemimysis*, and Female *Hemimysis* indicated there were significant effects of Date and Site on all subcategories (Table 5). Date*Site interactions were significant for all subcategories except juvenile *Hemimysis* and female *Hemimysis* (Table 5). Three-way ANOVA's run including Trap Number as an independent variable did not indicate that specific trap location effected *Hemimysis* catches. The observed effects all indicate that each subcategory of *Hemimysis* analyzed was more abundant at the GBW than at the REF. Overall, the total number of *Hemimysis* trapped at the GBW was approximately twice the catch at the REF (Fig. 8).

Bycatch in *Hemimysis* traps was extremely low (0.007% of catch) and consisted of only round goby fry, juvenile rusty crayfish, and *Echinogammarus ischnus*. Only one trap out of 119 total sets was fouled with sloughed cladophora.

Rock Collections

The invertebrate samples one-way ANOVAs indicated that both chironomid larvae and *Echinogammarus* abundance was statistically significant between sampling dates. The Tukey test statistic indicated that chironomid larvae were statistically in greater abundance in 2015 than either date in 2016 and that *Echinogammarus* were statistically more abundant in 2015 than both dates in 2016, while the 4 October, 2016 sample was also significantly greater than the 1 July, 2016 sample. During 2016, only one chironomid larvae was sampled from rock collections in July and none were sampled in October 2016.

DISCUSSION

Novel Breakwall Habitat

The breakwall of the Milwaukee Harbor creates a distinct interface between coastal Lake Michigan and the warmer estuarine Milwaukee Harbor. This sharp boundary is common throughout Great Lakes ports and harbors which are typically constructed around modified river mouths. The GBW and REF lie on the inside of the breakwall where it is typically warmer and experiences far less wave energy than the outside of the wall. The Milwaukee Breakwall's position and depth along such an interface allows for temporally and spatially diverse utilization of this unique rocky habitat by a number of native and introduced species from pelagic and nearshore ecosystems not known to overlap otherwise.

While rocky habitats are an important component of Great Lakes ecosystems and they are diverse (Janssen et al. 2005), the GBW and REF probably have no structural analog in nature. Rocky habitats vary and include glacially polished bedrock, glacial grooves in such bedrock typically infilled with cobble, talus slopes, and glacial deposits such as drumlins (Riley et al. 2014, 2017). Likely the best studied features are those used for spawning by lake trout and a key to their successful spawning is apparently suitable interstitial space for egg incubation (Marsden et al. 1995). Generally, this amounts to several layers of loose cobble overlying some impermeable substrate. The GBW and REF differ significantly from these natural features in that there are large interstitial spaces, or "caves", and the space between the quarried limestone boulders extends to the foundation on which they were deposited. Additionally, boulders of this size (6-10 tons) are quite uncommon throughout Lake Michigan and are likely only present in the form of glacial erratics exposed on the lake bed after centuries of erosion. Analogous groupings or drumlins with numerous boulders of this size are not known to exist naturally, thus the artificial caves created by their introduction may be an entirely unique feature responsible in part for the prolific *Hemimysis* population residing within them. The presence and diversity of caves likely explains the abundance of *Hemimysis* whose congeners include several lithophilic cave dwellers (Rastorgueff et al. 2011). This physically and hydrologically altered habitat and the unique mixture of native and introduced species interactions driving the local food web constitutes a novel ecosystem (Hobbs 2009).

The emerging food web at Milwaukee's Breakwall is driven by the introduced Ponto-Caspian mysid *Hemimysis anomala*, which is significantly more abundant at the GBW than at the REF (Table 5). *Hemimysis* were numerically the most abundant forage consumed by adult alewife, rainbow smelt, rock bass, and largemouth bass. *Hemimysis* were also the most frequently encountered food item in juvenile yellow perch diets. It was anticipated that emerging chironomid pupae would likely be the most common macroinvertebrate forage utilized by adult alewife based on their importance in other nearshore rocky habitats in Lake Michigan (Janssen and Luebke 2004; Waples et al. 2005; Kornis and Janssen 2011; Houghton and Janssen 2015). However, chironomid pupae accounted for less than 3% of adult alewife diet at both the GBW and REF and were no more than 4% of the diet of any other fish species encountered at the breakwall. Rock collections also indicate a significant decline in chironomids larvae at the GBW from 2015 to 2016 when none were collected (Table 6). While the reason for this decline is unclear, it may be partially driven by round gobies which often feed primarily on chironomid larvae (Lederer et al. 2006; Houghton and Janssen 2015). It is also possible that local competition for seston and predation by abundant *Hemimysis* may be negatively impacting their abundance at the GBW.

Elsewhere in the Great Lakes alewife, yellow perch, and rock bass are known to opportunistically prey on *Hemimysis* (Lantry et. al. 2010; Lantry et. Al. 2012). However, their ability to drive local food web dynamics of both pelagic and nearshore fishes has not previously been documented. Rainbow smelt gorging on abundant *Hemimysis* were regularly encountered at the GBW occupying water well above their thermal preferences during both gill netting and night dives in water as warm as 24.1°C, typically when cool water refugia were nearby due to upwelling events (Fig. 6A). Juvenile largemouth bass and rock bass at the GBW and REF also occupied habitat at the edge of their thermal preference with *Hemimysis* constituting >97% of their diets (Table 3). I believe the physical structure and hydrodynamics of the Milwaukee Breakwall has aided the proliferation of this benthopelagic macroinvertebrate to provide a seasonally abundant food source for both transient forage fish and their predators, while also creating forage and nursery habitat for the juveniles of nearshore resident gamefish.

Hemimysis Habitat

The GBW and REF distinct among natural rocky habitats and other artificial reefs where *Hemimysis* are known from in Lake Michigan, but shares common characteristics with each that I believe have facilitated *Hemimysis* utilization here. At shallow (~2m deep) natural reefs near a river mouth in Elk Rapids, MI *Hemimysis* use is most closely associated with loose cobble and high interstitial depths >20-30cm (Claramunt et. al. 2012). The shipping channel at the mouth Muskegon Lake from which *Hemimysis* were first identified in Lake Michigan is slightly deeper at ~10m, is positioned at the mouth of a fertile drowned river mouth lake where it is subject to periodic upwelling events, and the hardened shoreline of the channel consists primarily of loose rip-rap and cobble (Pothoven et al. 2007; Carl Reutz personal communication). The nearby artificial WE-Reef near Oak Creek, WI lies in 8-15m consisting of cobble and boulders with complex peaks and valleys, and is also subject to frequent upwelling events (Houghton 2014). Here *Hemimysis* were observed by research divers at the base of large boulders and while flipping loose cobble looking for round goby nests and during night dives (Janssen unpublished data). The physical structure of the GBW contains all of these characteristics on somewhat exaggerated scales. The GBW contains abundant deep interstices up to 3m deep with caves >2m^3 in volume in addition to countless smaller cavities of similar depth within the cobble. These diverse spaces deeper in the GBW may provide shelter from most benthic and pelagic predators as well as protection from high wave energy in an inherently turbulent breakwall zone. The GBW also lies at the mouth of the fertile estuary of the largest main basin tributary to Lake Michigan's western shore. Its position adjacent to Milwaukee Harbor's North gap also exposes the GBW to periodic upwelling events and frequent seiche driven currents.

I suggest that the modification of this boulder breakwall, specifically the addition of loose cobble with an abundance of deep and complex interstices, facilitates *Hemimysis* utilization. *Hemimysis* are crepuscular remaining in the shelter of rocks and cavities by day and has several congeners which closely associate with caves (Rastorgueff et al. 2011) so it is possible that a preference for the complex heterogeneous cavities in the GBW may be facilitating local success of *Hemimysis* as nearly twice as many adults and juveniles were caught at the GBW than at the REF. *Hemimysis* exhibited swarming behavior beginning in early August of both 2015 and 2016 and was continuously observed through November when field work ceased. *Hemimysis* were observed utilizing a variety of cavities which were nearly always sized relative to the size of the swarm or the individuals (i.e. Juveniles and small swarms utilizing smaller cavities than adults under similar densities). Large cavities may be less preferred by small swarms or juveniles as increased relative predation risk and cost of evasion efforts outweigh defensive benefits (Treisman 1975). At low densities and as juveniles *Hemimysis* were observed making use of the smaller heterogeneous cavities (2-20cm) of the GBW rather than the larger cavities of the boulder breakwall (0.5-2m).

An opportunistic omnivore, *Hemimysis* have been shown to incorporate energy from a variety of energy and carbon pathways in the Great Lakes including detrital, pelagic, and benthic periphyton (Marty et. al. 2010; Marty et. al. 2012; Ives et. al. 2013). During night dives *Hemimysis* were frequently observed in close association with the benthos likely foraging on the periphytic diatoms encrusting *Cladophora* growth, rocks, and mussel beds of the breakwall. This behavior was also recorded on video in September of 2015 as a swarm of *Hemimysis* fed on a fragment of diatom encrusted *Cladophora* dropped into the swarm by a snorkeler. Fecal pellet examination confirmed the frustule fragments of several periphytic diatoms, *Fragilaria* sp. and *Tabellaria* sp., as well as fragments of numerous pennate diatoms. Stable isotope analysis by Ives et al. (2013) in Lake Ontario did indicate that benthic periphyton can indeed be the primary carbon pathway used by *Hemimysis* at some locations. Fecal pellets also revealed head capsules of first instar chironomids larvae and cladoceran fragments (likely *Bosmina longirostris*). This suggests some connection with the pelagic food web although adult *Hemimysis* were never observed >1.5m above the benthos during night or daytime diving. *Hemimysis* feeding on zooplankters at the Milwaukee Breakwall may benefit from periodic upwellings and frequent seiche events which divers often observed concentrating zooplankton along both vertical and horizontal thermoclines intersecting the Breakwall. The presence of an abundant forage base of periphytic diatoms and zooplankton production inside the harbor have likely contributed to the success of this prolific *Hemimysis* population.

Nearshore and Estuarine Resident Fishes

Rock bass

Rock bass were the most abundant resident fish observed both in gill netting and during night dives at the GBW and REF. Rock bass were anticipated to be one of the primary resident fishes because of their inherent preference for rocky habitats, and the cover afforded them by complex cavitied present at the breakwall. Occupation of the Milwaukee Breakwall by resident rock bass is also likely due to important forage such as crayfish favoring rocky habitats. In both cases the physical structure of the breakwall may appeal to resident rock bass both as cover and as potential foraging grounds. Rock bass diets sampled from the breakwall indicate the preference for abundant *Hemimysis* forage was most likely a driving factor in their utilization of the GBW. *Hemimysis* were the primary forage item at both sites (REF: P_i

=0.87, GBW: P_i =0.97). Dissection of several rock bass caught in May 2015 indicated that *Hemimysis* were an important diet component despite the absence of *Hemimysis* observations during day time snorkeling and diving until late summer. Rock bass may thus be effective biosamplers elsewhere in the Great Lakes to indicate the presence and abundance of this elusive mysid prey (Lasley-Rasher et. al. 2015). Rock bass are likely the most well equipped native fish to forage on *Hemimysis* as their eyes are also well evolved to forage on other crepuscular benthic invertebrates such as crayfishes (Williamson and Keast 1988). The second major prey item of rock bass at both study sites were juvenile round gobies which tended to be consumed by larger rock bass although no clear shift to piscivory was observed. Interestingly, rusty crayfish which were anticipated to be of high importance to rock bass were found infrequently in their diet at the GBW and REF. It is possible that the inclusion of *Hemimysis* in the diets of these juvenile rock bass may compensate for the availability of suitable crayfish forage at the breakwall. Rock bass netted at the GBW were generally smaller than those found at the REF although the difference was not statistically significant. Night dive observations also confirmed that many of the rock bass occupying the GBW were smaller than those at the REF. This relationship is likely in response to the size of interstices and cavities in the smaller cobble at the GBW and large boulders at the REF used during the daytime as cover.

During both years of this study no rock bass were observed on the surface of the GBW or REF during any daytime dive or snorkel. Rock bass appear to heavily utilize the numerous deep interstices in the breakwall as cover, emerging at dusk to feed. Analysis of night dive rock bass observations indicated that rock bass utilization of the breakwall was complex and related to the temperature along deep and shallow transects. Rock bass observations along shallow transects increased with water temperatures and were significantly greater at the GBW than the REF. Under isothermal conditions rock bass were found utilizing the entire depth range of the breakwall, but when a cool hypolimnion was present rock bass were rarely seen along deep transects. Rock bass are likely always present at the breakwall but their activity is closely linked to their thermal preferences, which at 20.7°C to 29.8°C often places the GBW at or below their lower avoidance threshold (Cherry et al. 1976; Coutant 1977). Divers observed that when a thermocline was present virtually all rock bass were in the warmer epilimnion and, for the GBW, they would be near the shallow boulder-cobble interface. If the water was cold due to upwelling, rock bass were scarce throughout. When the water was warm to the bottom rock bass at the REF could be found all the way to the bottom, while GBW rock bass were at the shallow boulder-cobble interface.

Yellow Perch

In Lake Michigan, yellow perch utilize rocky habitat for foraging at a variety of life stages as well as for spawning substrate (Janssen and Quinn 1985; Robillard and Marsden 2001; Janssen and Luebke 2004). A majority of the yellow perch gillnetted were YOY which had recently returned to shore, post-larval drift. As pelagic larvae in Lake Michigan YOY yellow perch feed primarily on zooplankton for several months (Dettmers et al. 2005), making the diet shift to benthic fish and invertebrates after they return to nearshore rocky habitats preferred by YOY yellow perch (Janssen and Luebke 2004). Pelagic forage items, particularly calanoid copepods, were still a dominant forage item for yellow perch (REF: P_i =0.54, GBW: P_i =0.66), but *Hemimysis* occurred more frequently than copepods in perch caught at both sites. Predictions that *Hemimysis* may negatively compete with larval and juvenile fishes for zooplankton forage may be mitigated by consumption of juvenile and adult *Hemimysis* by post-larval fishes such as yellow perch. Additionally, there is a low degree of spatial overlap between adult *Hemimysis* and larval yellow perch in Lake Michigan as the latter drifts pelagically for several months before growing to overcome currents and return to shore. YOY yellow perch recently returning to the Milwaukee Harbor following pelagic larval drift readily consumed recently hatched *Hemimysis* which at <2mm in length are similar in stature and mobility to pelagic copepod forage they may have previously encountered. Abundant juvenile *Hemimysis* may serve as a link to first benthic feeding behavior in YOY yellow perch during the critical period where fry return to the nearshore.

Historically, adult yellow perch are known to consume *Mysis diluviana*, which have limited spatial overlap with yellow perch in Lake Michigan, but may seasonally accessed by yellow perch foraging in deep water (Wells 1980). The new presence of nearshore mysid forage year round potentially offers localized food patches which over time could affect yellow perch feeding ecology.

Largemouth Bass

The presence of YOY largemouth bass at the breakwall was unexpected and offers some insight into juvenile fish habitat use within the harbor. As vegetated regions of the Milwaukee Harbor are rather scarce and patchily distributed (Brennan Dow, UWM ongoing research) largemouth bass may be forced to choose between complex macrophyte stands where competition may be high and food encounter rates are relatively low, and hardened dock wall and rip-rap shorelines where low complexity may expose them to predation and make foraging in the open difficult. However, juvenile largemouth bass fortunate to encounter dense *Hemimysis* swarms in rocky habitats such as the GBW and REF may have high prey encounter rates resulting in a narrow diet when foraging optimally in a relatively less complex habitat to macrophyte stands (Anderson 1984). Largemouth bass in Milwaukee harbor are known to spawn at several locations greater than two shoreline miles away from the GBW and REF with primarily dock walls and hardened shorelines in between. Additionally, summer temperatures experienced at the breakwall are significantly below the thermal preference for YOY largemouth bass of 26.5°C to 32°C (Coutant 1977). *Hemimysis* were the primary forage item for YOY LMB comprising 98% of the food items consumed. The presence of *Hemimysis* in the rip-rap and boulders along hardened shorelines of the harbor may provide a unique forage connectivity with cover in the large rock cavities rather than vegetative cover and connections found in a more natural lake or drowned river mouth. Growth rates of YOY LMB consuming *Hemimysis* at the breakwall in September 2016 were also high with most individuals measuring >20mm longer than is typical for YOY LMB at this time of year in the Great Lakes region. While temperatures at the GBW may not typically be suitable for largemouth bass it could be expected they would potentially behave much like the rock bass at the GBW if temperatures were in their preferred range due to their similar foraging preferences. Although the potential for habitat overlap between these two species elsewhere in Lake Michigan is low, *Hemimysis* appear to offer a high value food resource for juvenile LMB where they can access them.

Transient Forage Fishes

Alewife

The presence of abundant alewife at the GBW was anticipated at the start of this study due to recent literature linking alewife preference over rocky habitats to chironomid emergence events in coastal waters (Janssen and Luebke 2004; Kornis and Janssen 2011; Houghton and Janssen 2015). At the GBW, a number of factors may have initially attracted alewife to the harbor such as inshore spawning migrations and their preference for foraging over rocky habitats. In each case the physical habitat was likely the initial cue attracting alewife to this new rocky habitat, while the abundant *Hemimysis* forage they encountered there was ancillary to their continued occupation of the breakwall. Prior research on the utilization of *Hemimysis* by pelagic prey fishes in the Great Lakes has focused on alewife, an effective predator on *Mysis diluviana,* an important native profundal mysid (Janssen and Brandt 1980, Walsh et al. 2008). At both the GBW and REF *Hemimysis* were numerically the most consumed forage item by adult alewives comprising 55% and 44% of food items respectively with most individuals gorging themselves with dozens of *Hemimysis* (Fig. 9). *Hemimysis* were also the most frequently consumed forage item by alewife during every month sampling occurred. *Hemimysis* accounted for greater than 85.6% of macroinvertebrates consumed by alewife at the Milwaukee Breakwall. This heavy utilization of *Hemimysis* forage by alewife is rather exceptional in the Great Lakes, and observations of alewife consuming *Hemimysis* are rather uncommon even in targeted diet studies (Lantry et. al. 2012; Yuille et.

al. 2012). Sampling done by Lantry et. al. (2010) is the only published survey in the Great Lakes to encounter a significant number of alewives consuming *Hemimysis* across several months of sampling. Neither the diet proportions of *Hemimysis* or the frequency at which *Hemimysis* occurred in alewife stomachs were significantly different between the GBW and REF. Because of the alewife's nature as a highly mobile and schooling feeder there may be some interference in signal from pelagic stomach contents consumed before foraging at the breakwall. Currents and thermal gradients which were observed by divers to concentrate zooplankton at the nearby North Gap may also have led to an over representation of zooplankters in alewife diets relative to *Hemimysis* which are only found in association with the rocky habitats sampled.

Juvenile alewife consumed *Hemimysis* at much lower rates than their adult counterparts and instead foraged primarily on zooplankton. *Hemimysis,* like many mysids, possess a strong evasive response to suction to avoid consumption and may be comparatively much harder to capture for small alewife as they are for other fishes (Fitzsimons et al. 2012). First mysid foraging by alewife in the Great Lakes may be learned during their first winter as they migrate offshore and encounter *Mysis diluviana*, thus adults may be more adept to catching this elusive food item than inexperienced juveniles.

Rainbow Smelt

While alewife foraging is linked to physical habitat in Lake Michigan, rainbow smelt foraging has not been linked to physical habitats in prior diet research (Crowder et al. 1981). Like alewife, rainbow smelt may initially be attracted to the Milwaukee Harbor during inshore spawning migrations where they encounter a rich patch of preferred mysid forage as they enter the harbor. As nearshore waters warm, rainbow smelt may consequently be excluded from the breakwall and *Hemimysis* forage until cold water upwelling currents entering the harbor create both refugia and access to abundant *Hemimysis* there. It appears that the presence of rainbow smelt in Milwaukee Harbor during summer is driven almost exclusively by *Hemimysis* forage as they were encountered in over 90% of rainbow smelt captured at both GBW and REF. *Hemimysis* accounted for 99.5% of all macroinvertebrates consumed at the GBW and 95.3% of those consumed at the REF. Rainbow smelt appear to have a strong preference to both occupy and forage at the cobble of the GBW over the boulders at the REF. Both gill net catch and night dive observations confirmed about twice as many rainbow smelt utilizing the GBW than the REF. Those individuals caught in gill nets were also found to have twice as many *Hemimysis* per stomach as rainbow smelt caught at the REF (Fig. 10). While the mechanism for this significant difference in foraging success is not clear, it may be that rainbow smelt forage more efficiently along the more even cobble slope than across large boulders and cavities where they may be exposed to predation themselves. It may also be that the smaller swarm sizes present at the GBW's small cavities reduce the defensive effects of *Hemimysis* swarming behavior leaving them more vulnerable to rainbow smelt predation. This increased consumption of *Hemimysis* by rainbow smelt at the GBW roughly corresponds with *Hemimysis* trap samples with approximately twice as many caught per trap at the GBW than at the REF.

Historically rainbow smelt in Lake Michigan's southern basin are found occupying the base of the thermocline between 10-30 meters typically in water between 7-15°C during the summer (Wells 1968; Crowder et. al. 1981). Rainbow smelt vertically migrate to feed at dusk in both estuaries and the ocean to forage on elusive prey such as copepods and mysids (Dauvin and Dodson 1990; Sirois and Dodson 2000), and also do so in inland lakes (Appenzeller and Leggett 1995). In the Great Lakes, they historically took advantage of abundant *Mysis diluviana* and are known to vertically migrate (Brandt et. al. 1980; Crowder et al. 1981). During night dives rainbow smelt at both GBW and REF were often observed closely associated with the benthos typically when a thermocline was present. On 9/6/2016 a school of smelt was observed occupying a thin layer of hypolimnetic water at the base of the GBW and REF passively riding the currents of the developing upwell into the harbor where they could access the rich cornucopia of *Hemimysis* at the breakwall. Rainbow smelt were also observed multiple times foraging at temperatures well above their thermal preference as high as 24.1°C. The sporadic thermal fluctuations at the breakwall yield a unique circumstance where rainbow smelt may be laterally migrating from cooler waters outside the breakwall to spend time foraging on a rich food resource under potentially lethal temperatures. Such behavior by fish is not undocumented (Janssen and Giesy 1984), but is infrequent under naturally occurring thermal gradients. Because of the local reliance of rainbow smelt on *Hemimysis*, the GBW may serve as a conditional biological-sink concentrating fish from less forage rich habitats present over a larger area (Loreau et al. 2013).

Round Goby

Round gobies were the most abundant resident fish captured in gill nets and observed while snorkeling and diving. At the GBW, they are found occupying cavities between rocks and feeding heavily on the *Dreissenid* mussels attempting to colonize the GBW. The relative abundance of round gobies caught in baited minnow traps was significantly greater at the GBW (Fig. 5), likely due to their preference for rocky cavities and abundance of nesting habitat there (Janssen and Jude 2001). Although *Hemimysis* were not a frequently encountered diet item for round gobies, divers observed numerous interactions between these species primarily during night dives. Round gobies were frequently seen occupying small cavities and the surface of the GBW attempting to capture *Hemimysis* which were swarming across the benthos all around them. Diet analysis of round goby foraging on *Hemimysis* was very similar to that reported by Fitzsimons et al. (2012) where round gobies were found to be an extremely ineffective predator on *Hemimysis.* I found only 12 of the 339 round gobies examined had successfully captured *Hemimysis.* While round gobies pose little predation pressure on *Hemimysis* foraging benthically at night, it is possibly that the frequent failed attacks observed during night dives may displace *Hemimysis* from small interstices and make them more vulnerable to predation by other fishes.

Juvenile Salmonids

Although catches of juvenile rainbow trout and brown trout were low, diet analysis indicates that they may feed heavily on *Hemimysis,* consuming several hundred at a time. During several night dives juvenile rainbow trout were also observed occupying large cavities at the GBW and adjacent REF where they behaved much like rainbow smelt apparently foraging along the edges of large swarms farther back in the shelter of the caves. Elsewhere in Lake Michigan this interaction may be more important, as *Hemimysis* present at the mouth of drowned river mouth lakes such as Muskegon Lake may become the first mysid forage for naturally reproducing salmon and trout out-migrating to the lake.

Conclusion

By any measure of abundance, the four most abundant species at the GBW were alewife, round goby, rainbow smelt, and rock bass. All four of these species have significantly different feeding ecology, habitat preferences, thermal niches, and native homelands. Yet the unique physical structure and abundant *Hemimysis* forage at the Milwaukee Breakwall facilitates their cohabitation of a completely artificial habitat. The results of this study, specifically night dive observations indicate that there is some degree of habitat partitioning driven by thermal preference and feeding ecology. Rainbow smelt, alewife, and rock bass are simultaneously present and feeding primarily on *Hemimysis* while occupying different portions of the GBW. Rock bass and rainbow smelt were closely associated with the benthos and segregated by thermal niche and depth, while alewife poorly adapted for benthic foraging took advantage of *Hemimysis* foraging away from the rocks and the other benthic predators.

Following the discovery of *Hemimysis* in the Great Lakes there was much speculation over their potential to alter nearshore energy pathways and food webs. Results of this study indicate that it is indeed possible for locally abundant *Hemimysis* population to drive food web dynamics and alter fish foraging behaviors, although the scale and importance of these effects beyond the local food web remains to be seen. Given *Hemimysis* specific habitat preferences and the uniqueness of the GBW's physical characteristics among rocky habitat in Lake Michigan it is unlikely to see such effects outside rocky breakwalls and harbors in the Great Lakes. The presence of a nearshore mysid species may also provide forage continuity never before seen in the Great Lakes between nearshore and pelagic habitat. Fishes such as alewife, rainbow smelt, juvenile salmonids, and coregonids which prefer mysid forage may now encounter them across much wider depth and habitat gradients facilitating long term changes in feeding ecology of potential *Hemimysis* predators. This bentho-pelagic macroinvertebrate also has a strong potential to become a locally important energy subsidy for alewife during inshore migrations as well as for juveniles of nearshore species. Where abundant, *Hemimysis* may also serve to further concentrate declining prey fish into areas where they are more vulnerable to predation to the detriment of these fish. The strength and importance of these localized effects has yet to be determined on a lake-wide scale as the distribution and abundance of *Hemimysis* in Lake Michigan is poorly understood.

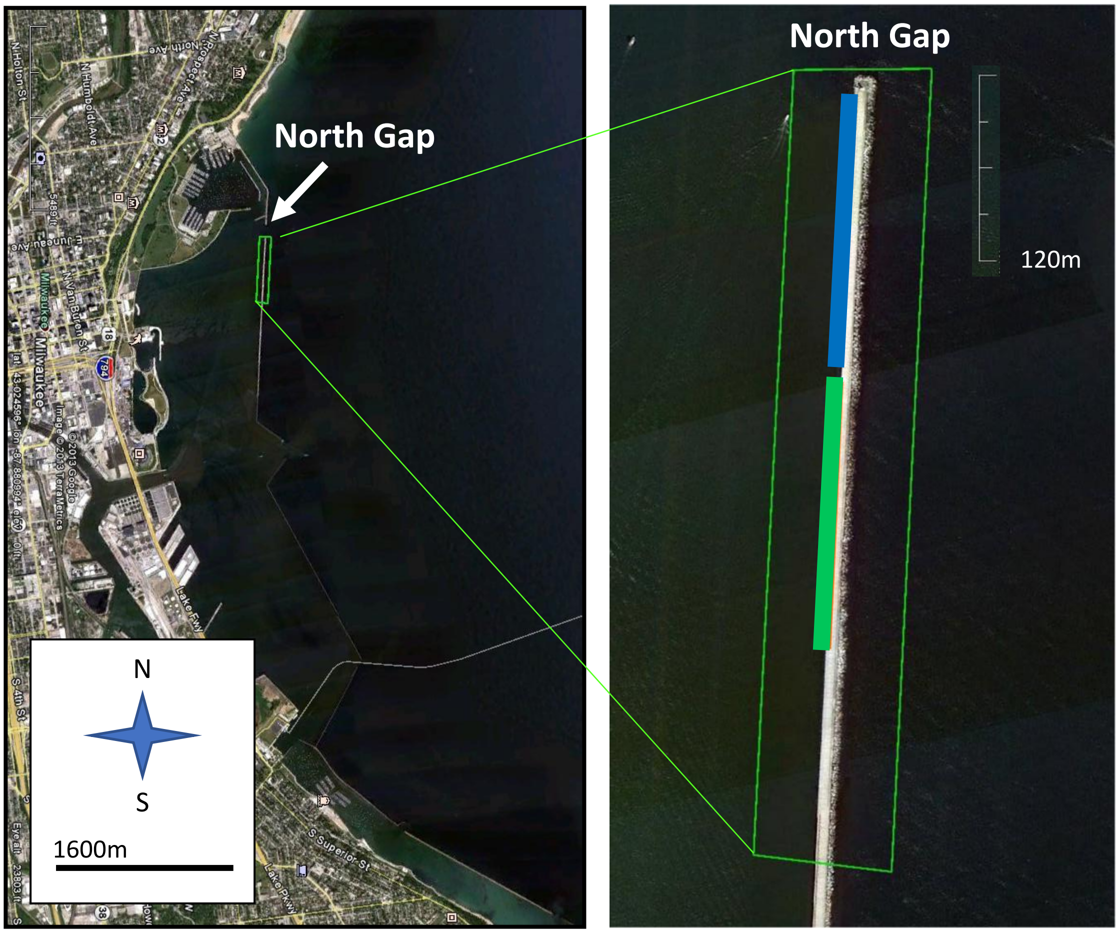

FIG. 1. Aerial view of Milwaukee Harbor (left) showing the breakwalls that separate the outer harbor from Lake Michigan. The study area (boxed right) with the location of the Milwaukee Harbor Green Breakwall (GBW) highlighted in green and the Reference Site (REF) highlighted in blue.

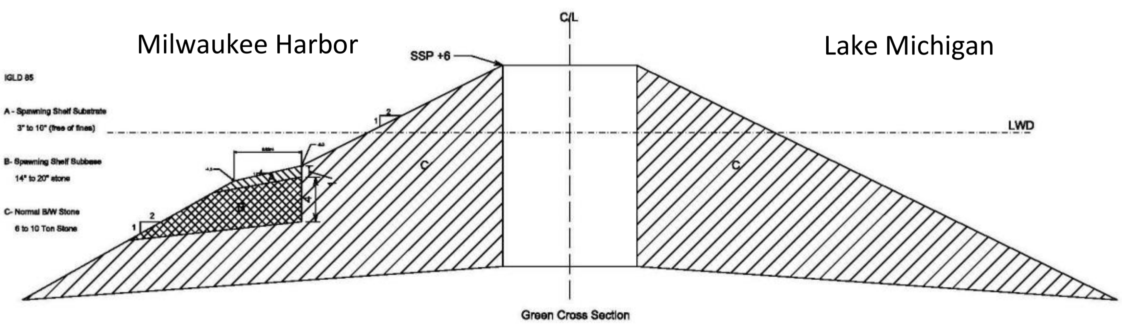

FIG. 2. Cross section of the plan for construction of the GBW and fish spawning inlay. Standard 6-10 ton armor-stone boulders indicated with “C”. Cobble “B” used to replace armor-stone includes 20-45cm stone, and the proposed spawning inlay “A” comprised of 10-20cm stone at the top of the GBW. Mean lake elevation is indicated by the dashed line.

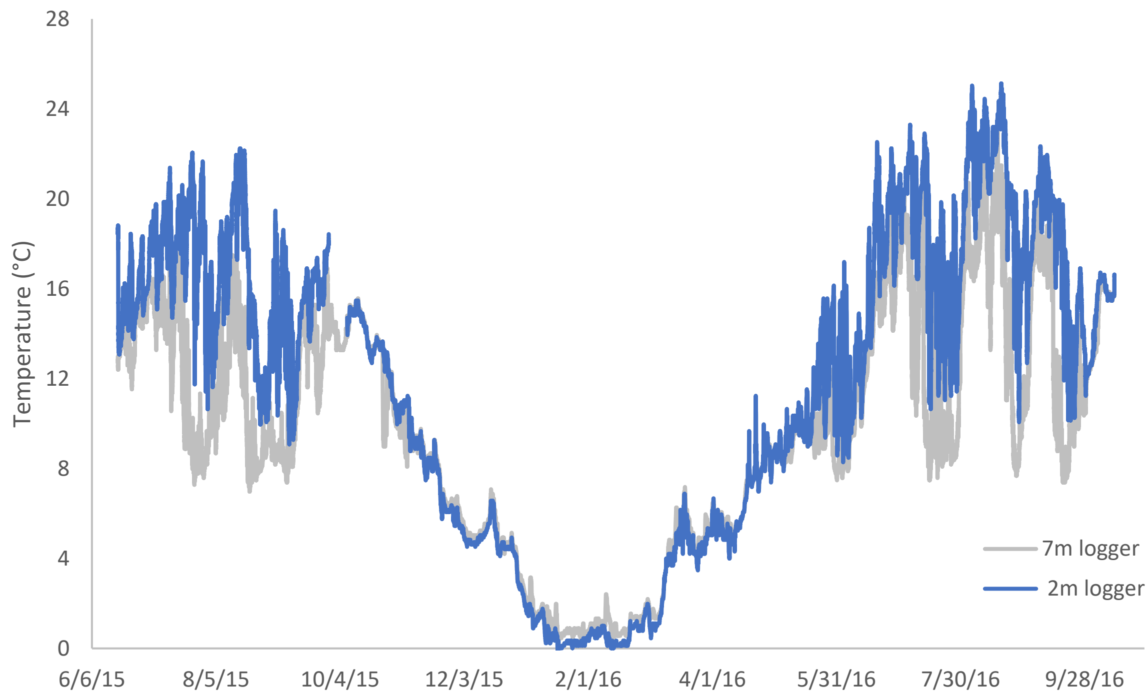

FIG. 3. Thermal profile recorded by HOBO pendant temperature loggers at depths of 2m and 7m at the interface between the GBW and REF.

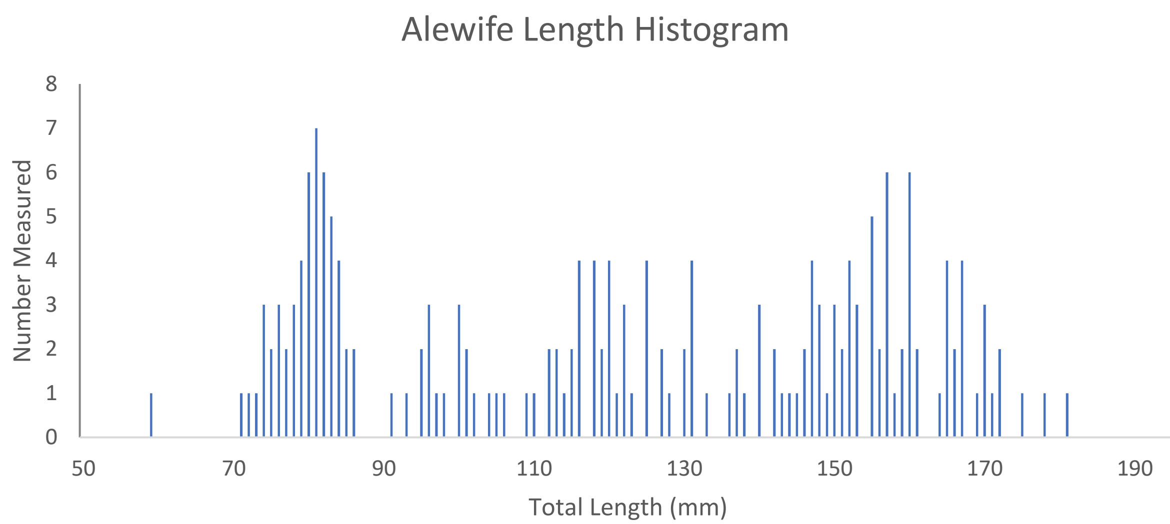

FIG. 4. Alewife total length(TL) Histogram from fish subsampled in 2016 indicating a year class of age <1 alewife between 70mm and 90mm TL

TABLE 1. Total gillnet catches from 2015 and 2016 at the GBW and REF.

	GBW			REF		
Species	2015	2016	Total	2015	2016	Total
Alewife	540	919	1459	620	1138	1758
Round Goby	384	429	813	278	385	663
Rainbow Smelt	6	328	334	6	150	156
Yellow Perch	2	77	79	6	88	94
White Sucker	37	1	38	48	1	49
Rock bass	46	2	48	24	7	31
Gizzard Shad	18	0	18	12	0	12
Largemouth Bass	2	13	15	3	2	5
Brown Trout	6	0	6	9	0	9
Walleye	2	0	2	4	0	4
Rainbow Trout	2	0	2	3	1	4
Lake Trout	2	0	2	0	0	0
Green Sunfish	1	1	2	0	0	0
Golden Shiner	1	0	1	0	0	0
Bluegill	1	0	1	0	0	0
Shorthead Redhorse	1	0	1	0	0	0
Common Carp	1	0	1	0	0	0
Spottail Shiner	0	0	0	0	1	1
Chinook Salmon	0	0	0	0	1	1
Freshwater Drum	0	1	1	0	0	0
Nine-spine Stickleback	0	1	1	0	0	0

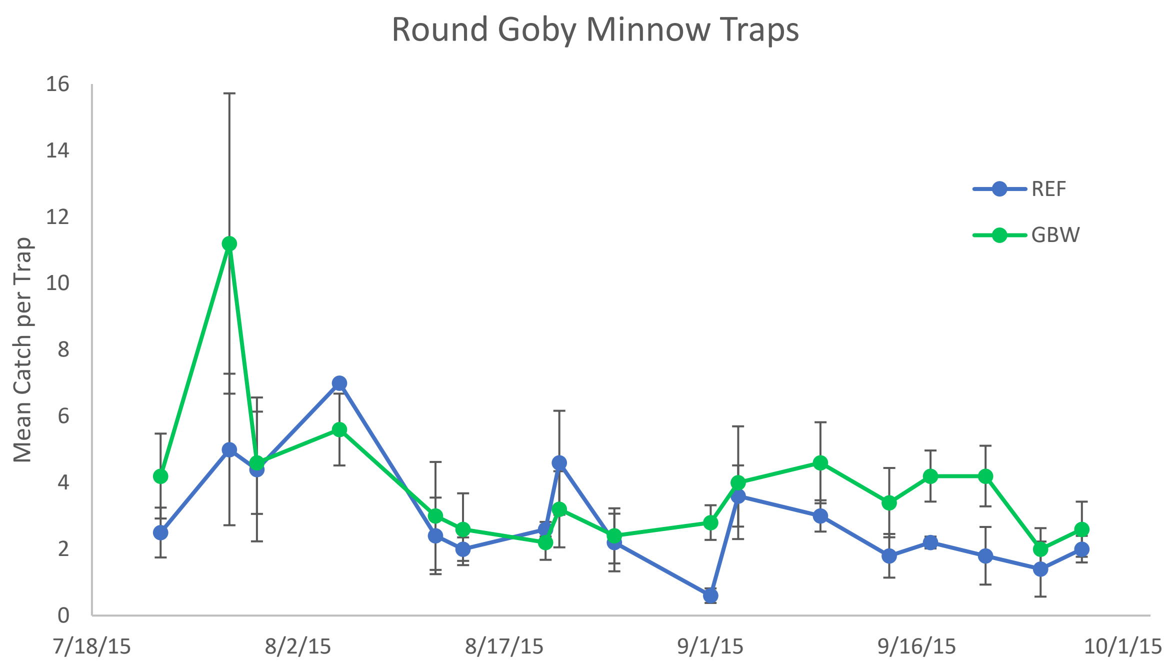

FIG. 5. Round goby catches from baited minnow traps set at the GBW and REF in 2015. Values are the mean ± S.E.

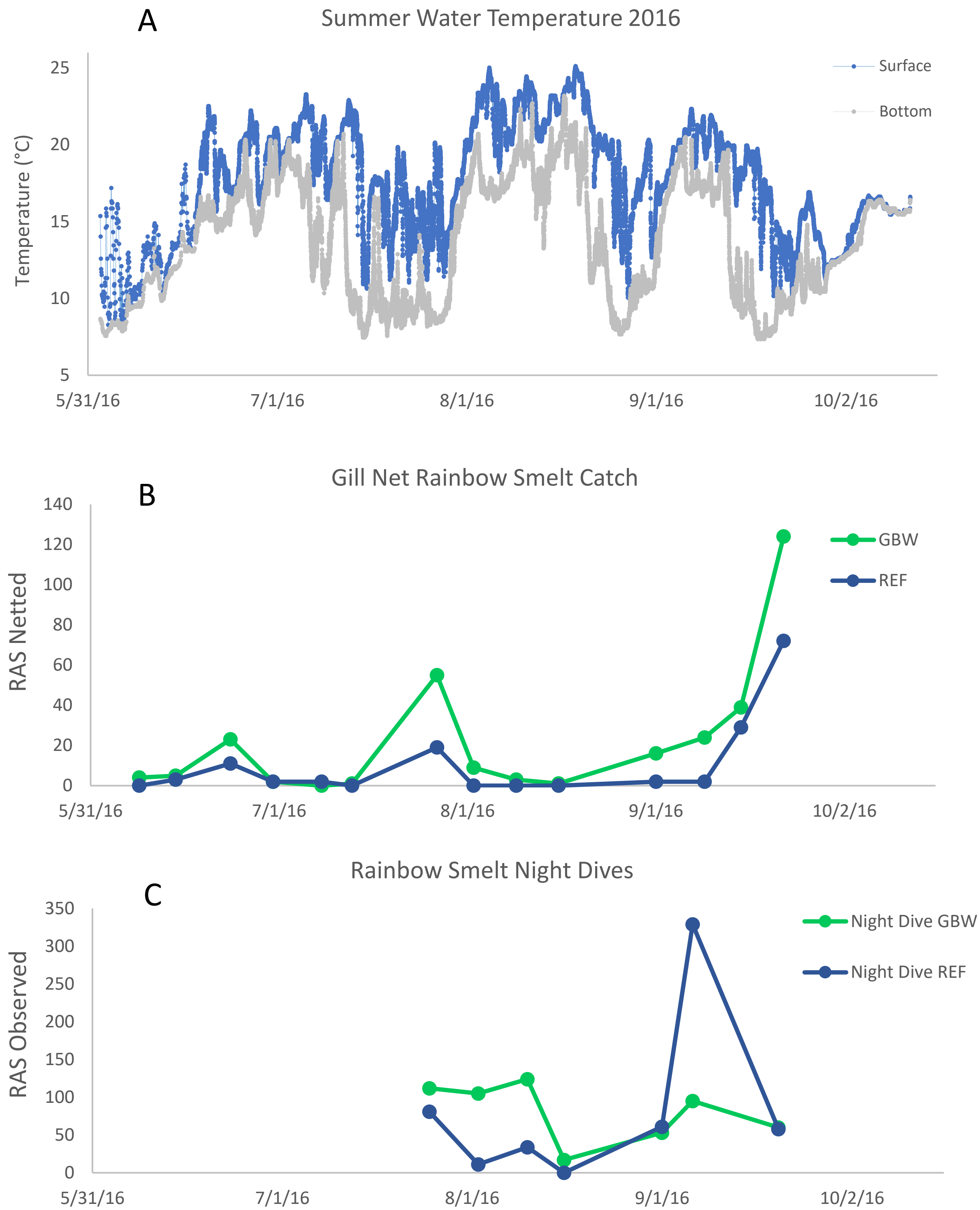

FIG. 6. A. Water temperatures at the GBW-REF interface during 2016 B. Rainbow smelt catch in gill nets C. Night dive observations of rainbow smelt

Prey Item	Juv Alewife		Adult Alewife		Round Goby		Rainbow Smelt		Yellow Perch		Rock Bass		Largemouth Bass	
	% F_i	P_i	% F_i	P_i	% F_i	P_i	% F_i	P_i	% F_i	P_i	% F_i	P_i	% F_i	P
MYSIDACEA														
Hemimysis anomala Adult	42	0.12	55	0.42	1	<0.01	88	0.41	60	0.23	43	0.85	100	0.85
Hemimysis anomala Juv	7	<0.01	16	0.02	0	0	26	0.05	47	0.21	5	0.02	20	0.13
CHIRONIMIDAE														
Chironomidae larvae	21	0.07	3	0.02	4	<0.01	0	0	6	0.01	0	0	0	0
Chironomidae pupae	51	0.06	38	0.03	16	0.04	14	0.02	17	0.01	19	0.02	20	0.02
CLADOCERA														
Bythotrephes longimanus	4	<0.01	10	0.02	2	<0.01	7	0.01	0	0	0	0	0	0
Bosmina longirostris	7	0.12	3	0.15	0	0	2	<0.01	0	0	0	0	0	0
Chydoridae	0	0	0	0	31	0.71	4	0.11	0	0	0	0	0	0
COPEPODA														
Calanoida	16	0.41	4	0.11	0	0	9	0.26	17	0.54	0	0	0	0
Unidentified Zooplankton	14	0.21	19	0.22	0	0	7	0.14	0	0	0	0	0	0
AMPHIPODA														
Echinogammarus ischnus	9	0.01	6	<0.01	11	0.01	7	<0.01	0	0	0	0	0	0
Gammarus sp.	0	0	0	0	2	<0.01	2	<0.01	0	0	0	0	0	0
DECAPODA														
Rusty Crayfish	0	0	0	0	1	<0.01	0	0	0	0	5	<0.01	0	0
DREISSENIDAE														
Dreissena sp.	0	0	0	0	79	0.22	0	0	0	0	0	0	0	0
Veliger	2	<0.01	1	0.01	0	0	2	<0.01	0	0	0	0	0	0
FISH														
Round Goby	0	0	1	<0.01	0	0	4	<0.01	17	<0.01	43	0.02	0	0
OTHER	0	0	0	0	15	0.02	2	<0.01	0	0	14	0.09	0	0
Number of fish examined	73		122		158		68		61		27		5	
Percent empty	22		21		25		16		13		22		0	
Mean TL(SD) in mm	78(8)		137(23)		73(18)		128(22)		95(42)		167(30)		52(8)	

TABLE 2. REF stomach contents from a subsample of fish caught during gill netting during 2015 and 2016. Prey items are measured in frequency of occurrence (%F_i) in fish without empty stomachs, and numerical proportion (P_i) of an item in the diet. Other taxa consumed at the REF included Hydropsychidae, Hydracarinidae, Harpacticoida, Isopoda, and terrestrial insects.

Prey Item	Juv Alewife $\%F_i$	Juv Alewife P_i	Adult Alewife $\% F_i$	Adult Alewife P_i	Round Goby $\% F_i$	Round Goby P_i	Rainbow Smelt $\% F_i$	Rainbow Smelt P_i	Yellow Perch $\% F_i$	Yellow Perch P_i	Rock Bass $\% F_i$	Rock Bass P_i	Largemouth Bass $\% F_i$	Largemouth Bass P_i
MYSIDACEA														
Hemimysis anomala Adult	37	0.07	71	0.53	6	0.01	88	0.54	53	0.10	59	0.97	44	0.09
Hemimysis anomala Juv	14	0.02	17	0.02	0	0	37	0.23	38	0.23	0	0	56	0.89
CHIRONIMIDAE														
Chironomidae larvae	22	0.03	13	0.04	21	0.07	2	<0.01	8	<0.01	4	<0.01	0	0
Chironomidae pupae	57	0.03	35	0.02	9	0.01	7	<0.01	18	<0.01	19	0.01	0	0
CLADOCERA														
Bythotrephes longimanus	3	<0.01	6	<0.01	0	0	1	<0.01	3	<0.01	0	0	0	0
Bosmina longirostris	6	0.08	7	0.13	0	0	1	0.01	0	0	0	0	0	0
Chydoridae	6	<0.01	1	<0.01	21	0.60	5	0.05	0	0.00	0	0	0	0
COPEPODA														
Calanoida	23	0.52	2	0.02	0	0	2	0.05	23	0.66	0	0	0	0
Unident. Zooplankton	18	0.22	10	0.23	0	0	7	0.11	0	0	0	0	0	0
AMPHIPODA														
Echinogammarus ischnus	3	<0.01	3	<0.01	10	0.02	1	<0.01	0	0	0	0	0	0
Gammarus	4	<0.01	0	0	1	<0.01	0	0	0	0	0	0	0	0
DECAPODA														
Rusty Crayfish	0	0	0	0	1	<0.01	0	0	0	0	15	<0.01	0	0
DREISSENIDAE														
Dreissena sp.	0	0	0	0	70	0.26	0	0	0	0	0	0	0	0
Veliger	9	0.02	1	<0.01	0	0	0	0	3	<0.01	0	0	0	0
FISH														
Round Goby	3	<0.01	0	0	0	0	0	0	18	<0.01	37	0.02	22	0.02
OTHER	0	0	1	<0.01	11	0.02	1	<0.01	0	0	0	0	0	0
Number of Stomachs	98		154		181		98		52		46		13	
Percent empty	19		22		30		17		23		41		31	
Mean length (SD)	76(9)		136(22)		73(26)		127(23)		81(29)		159(21)		74(22)	

TABLE 3. GBW stomach contents from subsamples of fish caught during gill netting in 2015 and 2016. Prey items are measured in frequency of occurrence ($\%F_i$) in fish without empty stomachs, and numerical proportion (P_i) of an item in the diet. Other taxa consumed at the GBW included Alewife, Hydropsychidae, Hydracarinidae, Harpacticoida, Isopoda, and diatoms.

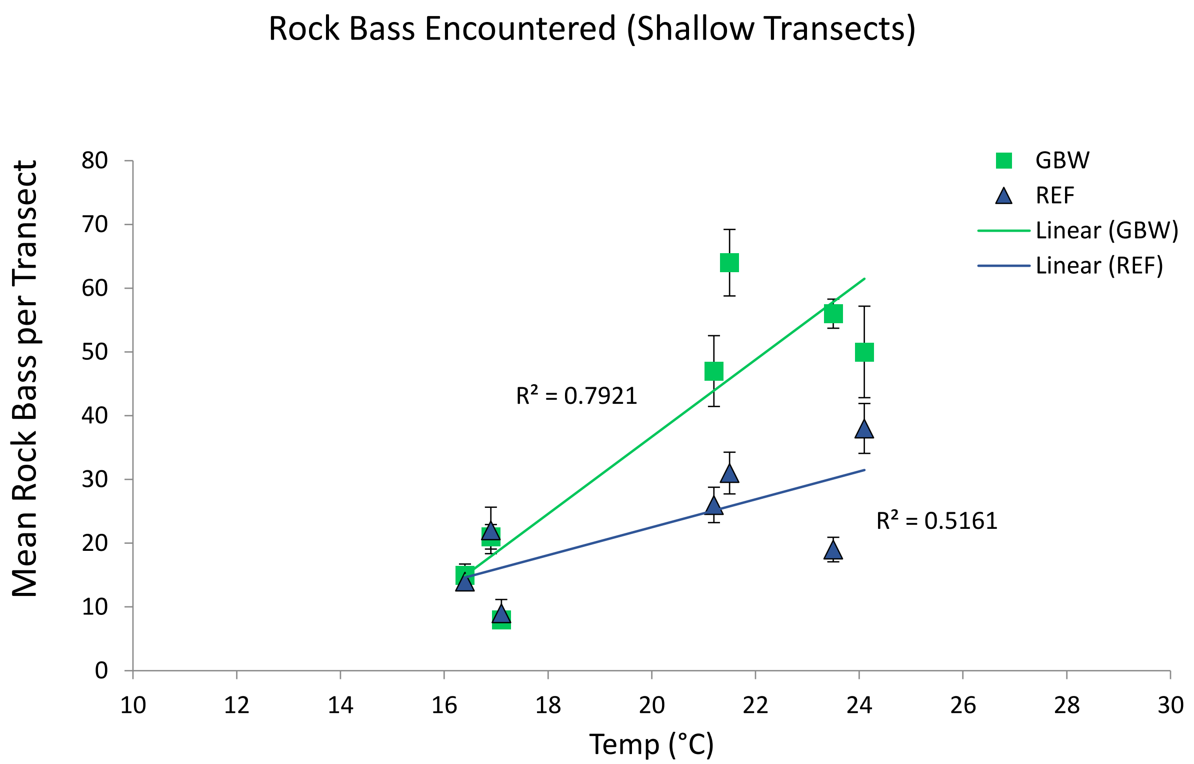

FIG. 7. Rock bass observed on the shallower transect of the GBW and REF during night dives in relation to temperature.

TABLE 4. Three-factor ANOVA analyzing the log(n+1) transformed number of rock bass and rainbow smelt observed on night dives in 2016.

		Rock bass Night			Rainbow Smelt Night		
Source	DF	F	P	Effect	F	P	Effect
Date	$F_{6, 112}$	14.3	**0.001**	**GBW>Ref**	8.58	**0.000**	**GBW>Ref**
Depth	$F_{1, 112}$	68.11	**0.001**	**Deep>Shal**	281.46	**0.000**	**Deep>Shal**
Site	$F_{1, 112}$	1.47	0.228	N.S.	4.99	**0.027**	**GBW>Ref**
Date * Depth	$F_{6, 112}$	5.93	**0.001**	**Deep>Shal**	7.44	**0.000**	**Deep>Shal**
Depth*Site	$F_{1, 112}$	8.19	**0.005**	**GBW>Ref**	14.79	**0.000**	**GBW>Ref**
Site * Date	$F_{6, 112}$	2.17	0.051	N.S.	6.93	**0.000**	**GBW>Ref**
Site*Depth*Date	$F_{6, 112}$	3.33	**0.005**	**GBW>Ref**	9.73	**0.000**	**GBW>Ref**

TABLE 5. *Hemimysis* Trap Two-factor ANOVA results

	Total *Hemimysis*		Adult *Hemimysis*		Juv *Hemimysis*		Male *Hemimysis*		Female *Hemimysis*	
Date	$F_{10,84}$ =	3.707	$F_{10,84}$ =	4.147	$F_{10,84}$ =	2.171	$F_{10,84}$ =	2.620	$F_{10,84}$ =	2.157
	p = 0.000	GBW>Ref	**p = 0.000**	GBW>Ref	**p = 0.027**	GBW>Ref	**p = 0.008**	GBW>Ref	**p = 0.028**	GBW>Ref
Site	$F_{1,84}$ =	6.805	$F_{1,84}$ =	5.567	$F_{1,84}$ =	6.230	$F_{1,84}$ =	8.347	$F_{1,84}$ =	4.930
	p = 0.011	GBW>Ref	**p = 0.021**	GBW>Ref	**p = 0.015**	GBW>Ref	**p = 0.005**	GBW>Ref	**p = 0.029**	GBW>Ref
Date*Site	$F_{10,84}$ =	2.744	$F_{10,84}$ =	2.667	$F_{10,84}$ =	1.598	$F_{10,84}$ =	2.328	$F_{10,84}$ =	1.512
	p = 0.006	GBW>Ref	**p = 0.007**	GBW>Ref	p = 0.121	N.S.	**p = 0.018**	GBW>Ref	p = 0.149	N.S.

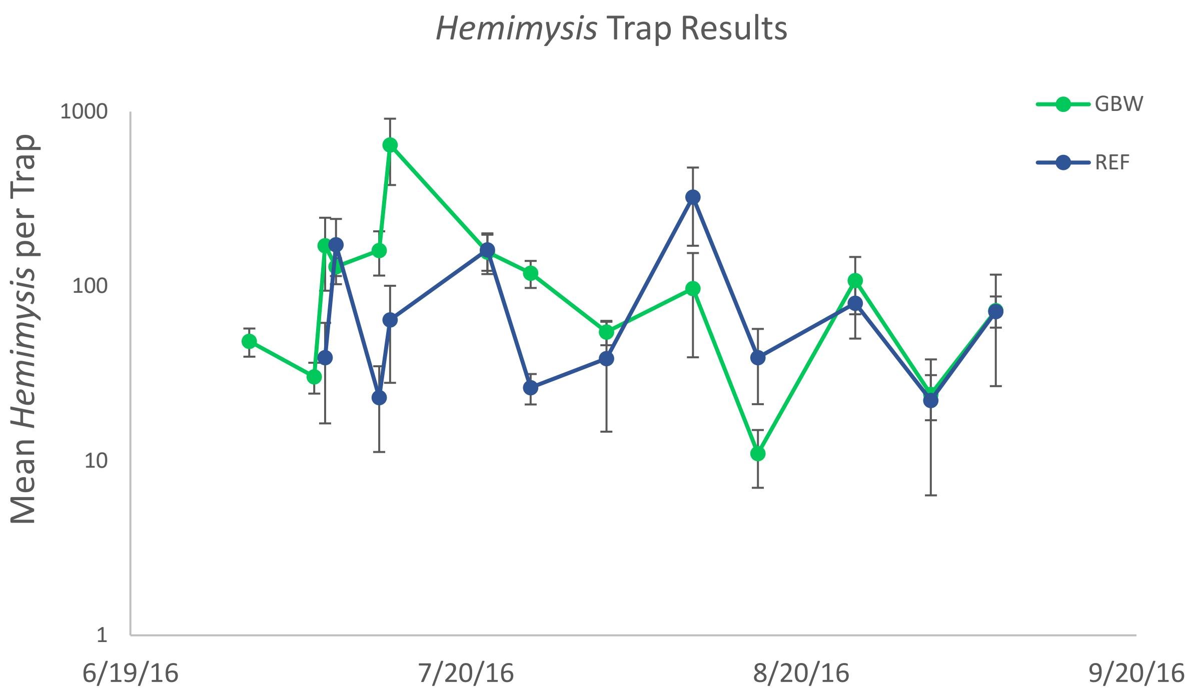

FIG. 8. *Hemimysis* trap results from 2016 sampling at the GBW and REF. Values are the mean ± S.E.

TABLE 6. Invertebrates captured on whole rock collections. Values are the mean ± standard deviation.

Date	Rocks Sampled	*Echinogammarus ischnus*	Chironomidae Larvae
9/24/2015	12	203.6±36.4	4.67±1.85
7/1/2016	12	18.1±4.7	0.08±0.08
10/4/2016	11	46.5±6.4	0±0

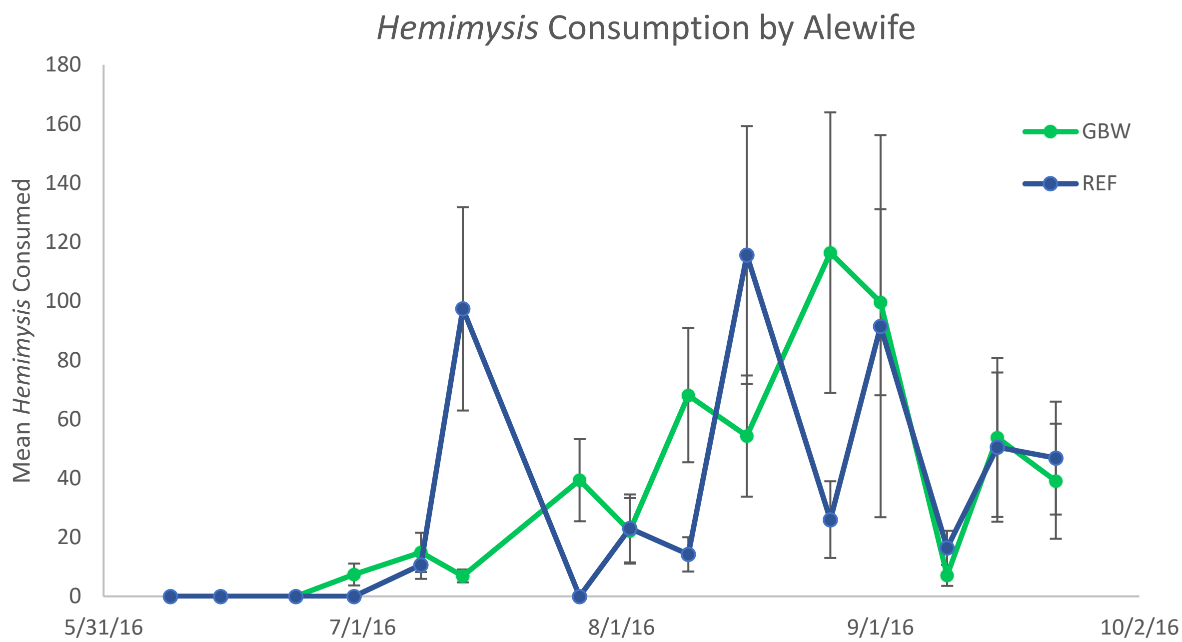

FIG. 9. Mean *Hemimysis* consumed per alewife sampled during 2016 micromesh gill netting efforts. Values are the mean ± S.E.

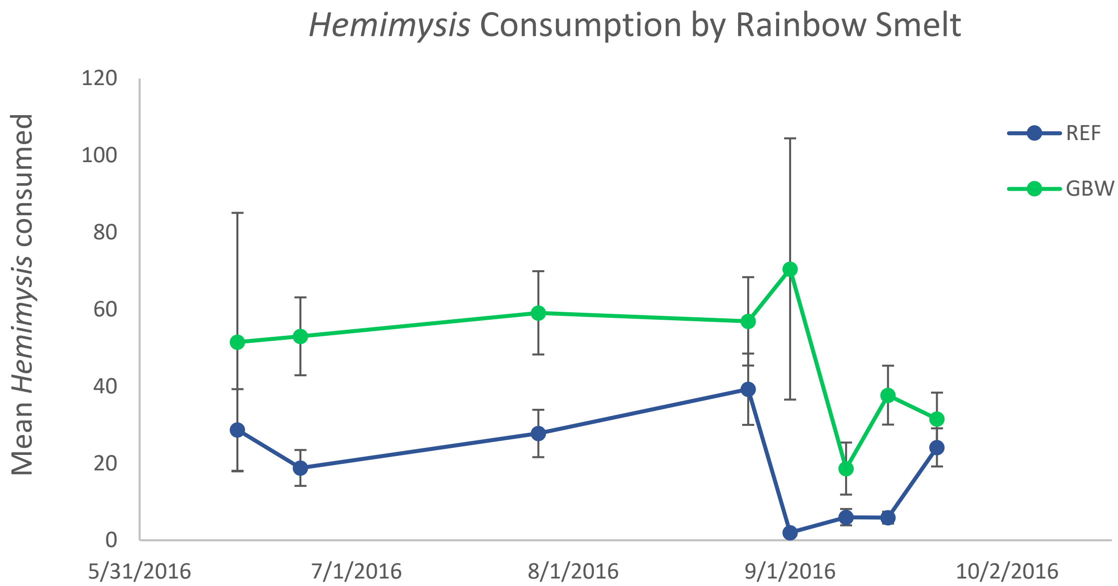

FIG. 10. Mean number of *Hemimysis* found in the stomachs of netted rainbow smelt in 2016. Values are the mean ± S.E.

WORKS CITED

Anderson, O., 1984. Optimal foraging by largemouth bass in structured environments. Ecology, 65(3), pp.851-861.

Appenzeller, A.R. and Leggett, W.C., 1995. An evaluation of light-mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt (*Osmerus mordax*). Canadian Journal of Fisheries and Aquatic Sciences, 52(3), pp.504-511.

Beletsky, D., Mason, D.M., Schwab, D.J., Rutherford, E.S., Janssen, J., Clapp, D.F. and Dettmers, J.M., 2007. Biophysical model of larval yellow perch advection and settlement in Lake Michigan. Journal of Great Lakes Research, 33(4), pp.842-866.

Borcherding, J., Murawski, S. and Arndt, H., 2006. Population ecology, vertical migration and feeding of the Ponto-Caspian invader *Hemimysis anomala* in a gravel-pit lake connected to the River Rhine. Freshwater Biology, 51(12), pp.2376-2387.

Brandt, S.B., Magnuson, J.J. and Crowder, L.B., 1980. Thermal habitat partitioning by fishes in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences, 37(10), pp.1557-1564.

Buckley, R.M., 1982. Marine habitat enhancement and urban recreational fishing in Washington. Marine Fisheries Review, 44(6), pp.28-37.

Cherry, D.S., Dickson, K.L., Cairns Jr, J. and Stauffer, J.R., 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. Journal of the Fisheries Board of Canada, 34(2), pp.239-246.

Claramunt, R.M., Barton, N.T., Fitzsimons, J.D. and Galarowicz, T.L., 2012. Microhabitat association of *Hemimysis anomala* on fish spawning reefs in Grand Traverse Bay, Lake Michigan. Journal of Great Lakes Research, 38, pp.32-36.

Coutant, C.C., 1977. Compilation of temperature preference data. Journal of the Fisheries Board of Canada, 34(5), pp.739-745.

Creque, S.M., Raffenberg, M.J., Brofka, W.A. and Dettmers, J.M., 2006. If you build it, will they come? Fish and angler use at a freshwater artificial reef. North American journal of fisheries management, 26(3), pp.702-713.

Crowder, L.B., Magnuson, J.J. and Brandt, S.B., 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Canadian Journal of Fisheries and Aquatic Sciences, 38(6), pp.662-668.

Crumpton, J.E. and Wilbur, R.L., 1974. Florida's fish attractor program. In Proceedings of the International Conference on Artificial Reefs, Houston. L. Colunga and R. Stone (Eds). TAMU-SG-74-103. Texas A & M University Sea Grant College, College Station, TX (p. 152).

Cuhel, R.L. and Aguilar, C., 2013. Ecosystem transformations of the Laurentian Great Lake Michigan by nonindigenous biological invaders.

Dauvin, J.C. and Dodson, J.J., 1990. Relationship between feeding incidence and vertical and longitudinal distribution of rainbow smelt larvae (*Osmerus mordax*) in a turbid well-mixed estuary. Marine ecology progress series. Oldendorf, 60: 1-12.

Dettmers, J.M., Janssen, J., Pientka, B., Fulford, R.S. and Jude, D.J., 2005. Evidence across multiple scales for offshore transport of yellow perch (*Perca flavescens*) larvae in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences, 62(12), pp.2683-2693.

D'Itri, F.M., 1986. Artificial reefs: marine and freshwater applications.

Fitzsimons, J.D., Bowen, K., Brousseau, C., Dalton, A., MacVeigh, B., Johnson, T.B. and Yuille, M., 2012. Round goby predation on *Hemimysis anomala*. Journal of Great Lakes Research, 38, pp.79-85.

Gerking, S.D., 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology, 34(2), pp.347-365.

Hobbs, R.J., Higgs, E. and Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. Trends in ecology & evolution, 24(11), pp.599-605.

Houghton, C.J. and Janssen, J., 2015. Changes in age-0 yellow perch habitat and prey selection across a round goby invasion front. Journal of Great Lakes Research, 41, pp.210-216.

Houghton, J.S., 2014. Great Lakes reefs: The good, the bad, the artificial (Doctoral dissertation, The University of Wisconsin-Milwaukee).

Ives, J.T., Marty, J., de Lafontaine, Y., Johnson, T.B., Koops, M.A. and Power, M., 2013. Spatial variability in trophic offset and food sources of *Hemimysis anomala* in lentic and lotic ecosystems within the Great Lakes basin. Journal of plankton research, 35(4), pp.772-784.

Janssen, J. and Brandt, S.B., 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences, 37(2), pp.177-184.

Janssen, J. and Giesy, J.P., 1984. A thermal effluent as a sporadic cornucopia: effects on fish and zooplankton. Environmental biology of fishes, 11(3), pp.191-203.

Janssen, J. and Quinn, J., 1985. Biota of the naturally rocky area of southwestern Lake Michigan with emphasis on potential fish prey. Artificial reefs: marine and freshwater applications. Edited by FM DiItri. Lewis Publishers, Chelsea, Mich, pp.431-442.

Janssen, J. and Jude, D.J., 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby Neogobius melanostomus. Journal of Great Lakes Research, 27(3), pp.319-328.

Janssen, J. and Luebke, M.A., 2004. Preference for rocky habitat by age-0 yellow perch and alewives. Journal of Great Lakes Research, 30(1), pp.93-99.

Janssen, J., Berg, M. and Lozano, S., 2005. Submerged terra incognita: the abundant but unknown rocky zones. The Lake Michigan Ecosystem: Ecology, Health and Management, pp.113-139.

Kelch, D.O., Snyder, F.L. and Reutter, J.F., 1999. Evaluation of artificial reefs as fish concentration devices in Lake Erie: Case studies of the Lorain and Lakewood, Ohio artificial reefs. In IAGLR'99. International Association for Great Lakes Research: Great Lakes, Great Science, Great Cities. Program and Abstracts.

Ketelaars, H.A., Lambregts-van de Clundert, F.E., Carpentier, C.J., Wagenvoort, A.J. and Hoogenboezem, W., 1999. Ecological effects of the mass occurrence of the Ponto–Caspian invader, *Hemimysis anomala* GO Sars, 1907 (Crustacea: Mysidacea), in a freshwater storage reservoir in the Netherlands, with notes on its autecology and new records. Hydrobiologia, 394, pp.233-248.

Kornis, M.S. and Janssen, J., 2011. Linking emergent midges to alewife (*Alosa pseudoharengus*) preference for rocky habitat in Lake Michigan littoral zones. Journal of Great Lakes Research, 37(3), pp.561-566.

Lantry, B.F., Walsh, M.G., Johnson, J.H. and McKenna Jr, J.E., 2010. Occurrence of the Great Lake's most recent invader, *Hemimysis anomala*, in the diet of fishes in southeastern Lake Ontario. Journal of Great Lakes Research, 36(1), pp.179-183.

Lantry, B.F., Gumtow, C.F., Walsh, M.G., Weidel, B.C., Boscarino, B.T. and Rudstam, L.G., 2012. Seasonal consumption of *Hemimysis anomala* by fish in Southeastern Lake Ontario, 2009–2010. Journal of Great Lakes Research, 38, pp.73-78.

Lasley-Rasher, R.S., Brady, D.C., Smith, B.E. and Jumars, P.A., 2015. It takes guts to locate elusive crustacean prey. Marine Ecology Progress Series, 538, pp.1-12.

Lederer, A., Massart, J. and Janssen, J., 2006. Impact of round gobies (*Neogobius melanostomus*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and the associated macroinvertebrate community across an invasion front. Journal of Great Lakes Research, 32(1), pp.1-10.

Loreau, M., Daufresne, T., Gonzalez, A., Gravel, D., Guichard, F., Leroux, S.J., Loeuille, N., Massol, F. and Mouquet, N., 2013. Unifying sources and sinks in ecology and Earth sciences. Biological Reviews, 88(2), pp.365-379.

Magnuson, J.J., Crowder, L.B. and Medvick, P.A., 1979. Temperature as an ecological resource. American Zoologist, 19(1), pp.331-343.

Marsden, J.E., Casselman, J.M., Edsall, T.A., Elliott, R.F., Fitzsimons, J.D., Horns, W.H., Manny, B.A., McAughey, S.C., Sly, P.G. and Swanson, B.L., 1995. Lake trout spawning habitat in the Great Lakes—a review of current knowledge. Journal of Great Lakes Research, 21, pp.487-497.

Marty, J., Bowen, K., Koops, M.A. and Power, M., 2010. Distribution and ecology of *Hemimysis anomala*, the latest invader of the Great Lakes basin. Hydrobiologia, 647(1), pp.71-80.

Marty, J., Ives, J., de Lafontaine, Y., Despatie, S., Koops, M.A. and Power, M., 2012. Evaluation of carbon pathways supporting the diet of invasive *Hemimysis anomala* in a large river. Journal of Great Lakes Research, 38, pp.45-51.

Moschella, P.S., Abbiati, M., Åberg, P., Airoldi, L., Anderson, J.M., Bacchiocchi, F., Bulleri, F., Dinesen, G.E., Frost, M., Gacia, E. and Granhag, L., 2005. Low-crested coastal defense structures as artificial habitats for marine life: using ecological criteria in design. Coastal Engineering, 52(10), pp.1053-1071.

Pothoven, S.A., Grigorovich, I.A., Fahnenstiel, G.L. and Balcer, M.D., 2007. Introduction of the Ponto-Caspian bloody-red mysid *Hemimysis anomala* into the Lake Michigan basin. Journal of Great Lakes Research, 33(1), pp.285-292.

Prince, E.D., Maughan, O.E. and Brouha, P., 1977. How to build a freshwater artificial reef.

Rastorgueff, P.A., Harmelin-Vivien, M., Richard, P. and Chevaldonné, P., 2011. Feeding strategies and resource partitioning mitigate the effects of oligotrophy for marine cave mysids. Marine Ecology Progress Series, 440, pp.163-176.

Ray, W.J. and Corkum, L.D., 2001. Habitat and site affinity of the round goby. Journal of Great Lakes Research, 27(3), pp.329-334.

Ricciardi, A. and MacIsaac, H.J., 2000. Recent mass invasion of the North American Great Lakes by Ponto–Caspian species. Trends in Ecology & Evolution, 15(2), pp.62-65.

Riley, S.C., Binder, T.R., Wattrus, N.J., Faust, M.D., Janssen, J., Menzies, J., Marsden, J.E., Ebener, M.P., Bronte, C.R., He, J.X. and Tucker, T.R., 2014. Lake trout in northern Lake Huron spawn on submerged drumlins. Journal of Great Lakes Research, 40(2), pp.415-420.

Riley, S.C., Binder, T.R., Tucker, T.R., Menzies, J., Eyles, N., Janssen, J., Muir, A.M., Esselman, P.C., Wattrus, N.J. and Krueger, C.C., 2017. Islands in the ice stream: were spawning habitats for native salmonids in the Great Lakes created by paleo-ice streams?. Fish and Fisheries, 18(2), pp.347-359.

Rogers, M.W., Bunnell, D.B., Madenjian, C.P. and Warner, D.M., 2014. Lake Michigan offshore ecosystem structure and food web changes from 1987 to 2008. Canadian Journal of Fisheries and Aquatic Sciences, 71(7), pp.1072-1086.

Rutecki, T.L., Dorr III, J.A. and Jude, D.J., 1985. Preliminary analysis of colonization and succession of selected algae, invertebrates, and fish on two artificial reefs in inshore southeastern Lake Michigan. Artificial reefs: marine and freshwater applications, pp.459-489.

Scyphers, S.B., Powers, S.P. and Heck, K.L., 2015. Ecological value of submerged breakwaters for habitat enhancement on a residential scale. Environmental management, 55(2), pp.383-391.

Sirois, P. and Dodson, J.J., 2000. Influence of turbidity, food density and parasites on the ingestion and growth of larval rainbow smelt *Osmerus mordax* in an estuarine turbidity maximum. Marine Ecology Progress Series, 193, pp.167-179.

Stone, R. B. 1974. A brief history of artificial reef activities in the United States. L Colunga and R. B. Stone, Proceedings of an international conference on artificial reefs, p. 24-27. Tex. A&M Univ. Sea Grant Rep. TAMU-SG-74-103.

Stone, R.B., 1982. Artificial reefs: Toward a new era in fisheries enhancement?. Marine Fisheries Review, 44(6), pp.2-3.

Taraborelli, A.C., Jakobi, N., Johnson, T.B., Bowen, K. and Boscarino, B.T., 2012. Distribution, abundance and production of *Hemimysis anomala* in Lake Ontario. Journal of Great Lakes Research, 38, pp.52-57.

Turschak, B.A., Bunnell, D., Czesny, S., Höök, T.O., Janssen, J., Warner, D. and Bootsma, H.A., 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology, 95(5), pp.1243-1252.

Treisman, M., 1975. Predation and the evolution of gregariousness. II. An economic model for predator-prey interaction. Animal Behaviour, 23, pp.801-825.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A. and Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences, 59(7), pp.1209-1228.

Walsh, M.G., O'Gorman, R., Strang, T., Edwards, W.H. and Rudstam, L.G., 2008. Fall diets of alewife, rainbow smelt, and slimy sculpin in the profundal zone of southern Lake Ontario during 1994–2005 with an emphasis on occurrence of Mysis relicta. Aquatic Ecosystem Health & Management, 11(4), pp.368-376.

Walsh, M.G., Lantry, B.F., Boscarino, B., Bowen, K., Gerlofsma, J., Schaner, T., Back, R., Questel, J., Smythe, A.G., Cap, R. and Goehle, M., 2010. Early observations on an emerging Great Lakes invader *Hemimysis anomala* in Lake Ontario. Journal of Great Lakes Research, 36(3), pp.499-504.

Waples, J.T., Paddock, R., Janssen, J., Lovalvo, D., Schulze, B., Kaster, J. and Klump, J.V., 2005. High resolution bathymetry and lakebed characterization in the nearshore of western Lake Michigan. Journal of Great Lakes Research, 31, pp.64-74.

Wells, L., 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. Fish. Bull, 67(1), pp.1-15.

Wells, L., 1980. Food of alewives, yellow perch, spottail shiners, trout-perch, and slimy and fourhorn sculpins in southeastern Lake Michigan (No. 98). US Fish and Wildlife Service.

Williamson, M. and Keast, A., 1988. Retinal structure relative to feeding in the rock bass (*Ambloplites rupestris*) and bluegill (*Lepomis macrochirus*). Canadian journal of zoology, 66(12), pp.2840-2846.

Yuille, M.J., Johnson, T.B., Arnott, S.E. and Campbell, L.M., 2012. *Hemimysis anomala* in Lake Ontario food webs: stable isotope analysis of nearshore communities. Journal of Great Lakes Research, 38, pp.86-92.